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CONTENTS OF VOLUME 8

CONTENTS

1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, pls. 1-2, 26 figs. in text, 17 tables. September 1, 1954.
2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figs. in text, 4 tables. November 15, 1954.
3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, pls. 3-6, 10 figs. in text, 9 tables. February 10, 1956.
4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figs. in text. February 10, 1956.
5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 fig. in text. March 10, 1956.
6. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figs. in text. April 2, 1956.
7. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. By Henry S. Fitch. Pp. 417-476, 10 figs. in text, 6 tables. June 1, 1956.
8. Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas. By Dwight Platt. Pp. 477-498, 4 tables. June 8, 1956.
9. Ecological observations on the woodrat, Neotoma floridana. By Henry S. Fitch and Dennis G. Rainey. Pp. 499-533, 3 figs. in text. June 12, 1956.
10. Eastern woodrat, Neotoma floridana: Life history and ecology. By Dennis G. Rainey. Pp. 535-646, 12 plates, 13 figs. in text. August 15, 1956.

Index. Pp. 647-675.

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UNIVERSITY OF KANSAS PUBLICATIONS
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Volume 8, No. 1, pp. 1-156, 2 pls., 26 figs. in text, 17 tables
September 1, 1954

Life History and Ecology of the Five-lined Skink, Eumeces fasciatus

BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
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Vol. 1.
1. The pocket gophers (Genus Thomomys) of Utah. By Stephen D. Durrant. Pp. 1-82, 1 figure in text. August 15, 1946.
2. The systematic status of Eumeces pluvialis Cope, and noteworthy records of other amphibians and reptiles from Kansas and Oklahoma. By Hobart M. Smith. Pp. 85-89. August 15, 1946.
3. The tadpoles of Bufo cognatus Say. By Hobart M. Smith. Pp. 93-96, 1 figure in text. August 15, 1946.
4. Hybridization between two species of garter snakes. By Hobart M. Smith. Pp. 97-100. August 15, 1946.
5. Selected records of reptiles and amphibians from Kansas. By John Breukelman and Hobart M. Smith. Pp. 101-112. August 15, 1946.
6. Kyphosis and other variations in soft-shelled turtles. By Hobart M. Smith. Pp. 117-124, 3 figures in text. July 7, 1947.

*7. Natural history of the prairie vole (Mammalian Genus Microtus). By E. W. Jameson, Jr. Pp. 125-151, 4 figures in text. October 6, 1947.

8. The postnatal development of two broods of great horned owls (Bubo virginianus). By Donald F. Hoffmeister and Henry W. Setzer. Pp. 157-173, 5 figures in text. October 6, 1947.
9. Additions to the list of the birds of Louisiana. By George H. Lowery, Jr. Pp. 177-192. November 7, 1947.
10. A check-list of the birds of Idaho. By M. Dale Arvey. Pp. 193-216. November 29, 1947.
11. Subspeciation in pocket gophers of Kansas. By Bernardo Villa-R. and E. Raymond Hall. Pp. 217-236, 2 figures in text. November 29, 1947.
12. A new bat (Genus Myotis) from Mexico. By Walter W. Dalquest and E. Raymond Hall. Pp. 237-244, 6 figures in text. December 10, 1947.
13. Tadarida femorosacca (Merriam) in Tamaulipas, Mexico. By Walter W. Dalquest and E. Raymond Hall. Pp. 245-248, 1 figure in text. December 10, 1947.
14. A new pocket gopher (Thomomys) and a new spiny pocket mouse (Liomys) from Michoacán, México. By E. Raymond Hall and Bernardo Villa R. Pp. 249-256, 6 figures in text. July 26, 1948.
15. A new hylid frog from eastern Mexico. By Edward H. Taylor. Pp. 257-264, 1 figure in text. August 16, 1948.
16. A new extinct emydid turtle from the Lower Pliocene of Oklahoma. By Edwin C. Galbreath. Pp. 265-280, 1 plate. August 16, 1948.
17. Pliocene and Pleistocene records of fossil turtles from western Kansas and Oklahoma. By Edwin C. Galbreath. Pp. 281-284. August 16, 1948.
18. A new species of heteromyid rodent from the Middle Oligocene of northeastern Colorado with remarks on the skull. By Edwin C. Galbreath. Pp. 285-300, 2 plates. August 16, 1948.
19. Speciation in the Brazilian spiny rats (Genus Proechimys, Family Echimyidae). By João Moojen. Pp. 301-406, 140 figures in text. December 10, 1948.
20. Three new beavers from Utah. By Stephen D. Durrant and Harold S. Crane. Pp. 407-417, 7 figures in text. December 24, 1948.
21. Two new meadow mice from Michoacán, Mexico. By E. Raymond Hall. Pp. 423-427, 6 figures in text. December 24, 1948.
22. An annotated check list of the mammals of Michoacán, Mexico. By E. Raymond Hall and Bernardo Villa R. Pp. 431-472, 2 plates, 1 figure in text. December 27, 1949.
23. Subspeciation in the kangaroo rat, Dipodomys ordii. By Henry W. Setzer. Pp. 473-573, 27 figures in text, 7 tables. December 27, 1949.

(Continued on inside of back cover)

UNIVERSITY OF KANSAS PUBLICATIONS
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LIFE HISTORY AND ECOLOGY OF THE FIVE-LINED SKINK, EUMECES FASCIATUS

By

Henry S. Fitch

Introduction

The common five-lined skink (or common blue-tailed skink) is a small woodland lizard, abundantly and widely distributed over the eastern United States. Many authors have casually discussed this lizard or have treated in detail some phase of its biology. Excellent brief summaries of the known facts concerning its life history have been published by Smith (1946:349-350 and 1950:187-188) and Pope (1947:153-157). Nevertheless, no thoroughgoing study of its life history and ecology has heretofore been made.

In 1932, taxonomic studies by Dr. Edward H. Taylor revealed that the lizards previously referred to in the literature as *Eumeces fasciatus,* actually were three closely related and similar, partly sympatric species. Although Taylor's work was careful and detailed, and indicated numerous minor differences by which the three species could be distinguished, many herpetologists were reluctant to accept his findings for nearly a decade thereafter. Consequently a large amount of literature concerning five-lined skinks is either obviously composite in the sense that it is based upon two or three species, or is not definitely assignable to any one species. In the study here reported upon, all pertinent literature available to me has been examined, and evaluated, and important findings of other authors have been incorporated in the discussion. However, mine was primarily a field study, and in one small part of the geographic range of the one species.

The University of Kansas Natural History Reservation is a tract of 590 acres preserved as a natural area, available for the pursuit of ecological studies. The studies undertaken include intensive investigations of selected species of vertebrate animals. The main criteria used in selecting these species have been whether or not they were sufficiently abundant and generally enough distributed to play an important role in the over-all ecology of the area, and whether a species was sufficiently accessible for study with available techniques. Among the 300 species of vertebrate animals recorded from the Reservation, the five-lined skink is one of those most frequently noticed in the field. In actual numbers it is probably exceeded only by the cricket frog (*Acris gryllus*), the leopard frog (*Rana pipiens*), the ring-necked snake (*Diadophis punctatus*), the prairie vole (*Microtus ochrogaster*) and perhaps the white-footed mouse (*Peromyscus leucopus*). Although numerous, the skink is not easy to study because it is secretive in its behavior, and is inactive in inaccessible shelters during the greater part of the year.

The five-lined skink generally occurs along with a characteristic set of community associates in a particular type of situation. It is a predator on various small animals, mostly invertebrates. For some of the many prey species the effect is certainly negligible, but for others its predation may be a major ecological factor. In areas where optimum habitat conditions exist its biomass may exceed that of any other insectivorous animal, and in such situations it assumes a major role as a predator and as a competitor with other insectivorous types. In turn it provides part of the food source of various larger predators, including reptiles, birds and mammals. It is a host and carrier of various parasites, including at least one species that regularly attacks humans—the common chigger. It is not evident on the basis of the present findings that the skink is either harmful or beneficial to any perceptible degree, in its over-all effect on human affairs and economy. Nevertheless, there probably are various unsuspected relationships.

In the course of my field study many workers on the University of Kansas Natural History Reservation helped by capturing skinks; especially Sydney Anderson, Richard Freiburg, John Hawken, Dennis G. Rainey and Lewis L. Sandidge. Mr. Robert Gordon very kindly furnished information on specimens in the Tulane University collection, which served as a basis for comparing the breeding schedule of the southern population with that of *E. fasciatus* in northeastern Kansas. Dr. W. J. Breckenridge kindly permitted examination of material in the University of Minnesota Museum of Natural History. Dr. Edward H. Taylor has made helpful suggestions from time to time. Mr. Richard B. Loomis helped me in various ways with the field work, and made available his personal field notes with records of predation on *Eumeces* by various snakes. Dr. E. Raymond Hall, Director of the Museum of Natural History, has critically examined the manuscript, and has been helpful in various ways. The line drawings and graphs, with the exception of Figures 8 and 9, were made or completed by Mrs. Louise Brunk, artist for the Museum.

The study here reported on was initiated in May 1949, and was continued through 1950, 1951 and 1952. A few observations made in 1948 have been included. Various separate items of information obtained in 1953 have likewise been incorporated especially where histories of individual skinks are presented, but the manuscript was completed in essentially its present form in the fall of 1952.

Methods

Skinks were obtained by active search; rocks and boulders were lifted up and the skinks thus exposed were seized by hand before they had time to escape. This method was effective when the skinks were using rocks for shelter and when temperatures were low enough so that they were slow and sluggish, but in hot weather the skinks were so quick and active that those exposed usually escaped. Usually skinks could be obtained much more easily by trapping. At the pond rock pile (Fig. 26), for instance, shelter was so readily available that the skinks could seldom be caught by hand. Gallon cans buried with the tops open flush with the surface of the ground served as pitfalls and were effective when they were carefully placed, at the bases of rock ledges or logs or stumps, where the skinks were most likely to fall into them. Most of the skinks recorded at the rock pile were caught by this method, and sometimes several were caught together in the same pitfall. Ordinarily each pitfall was covered with a large flat rock, propped against a nearby object to leave ample space for the skink to enter beneath it. The rocks provided protection from direct sunlight, from rain, and from predators. Still another method of catching skinks was with wire screen funnel traps (Fitch 1951:77). These funnel traps were of different sizes, and were made of different kinds of wire mesh. They were set for reptiles that were mostly larger than five-lined skinks, and those having quarter-inch wire mesh permitted many of the immature skinks to escape. Most of these funnel traps were from about one foot long and five inches in diameter, to about twice these dimensions, with funnel openings about 1.5 inches in diameter. Some made of ⅛ inch wire mesh, six or seven inches long, and three or four inches in diameter, with funnel openings only a little larger than the body diameter of an adult skink, were found to be suitable for skinks of all sizes, and were used successfully at the pond rock pile. Most of the skinks trapped were adult males, and they were taken chiefly in May. The funnel traps were generally placed at the edges of rock outcrops, boulders or logs, where skinks were likely to be intercepted in their usual travel routes. Each method of collecting skinks resulted in occasional mortality to them but most losses were in those caught in funnel traps. In these traps they sustained rapid loss of moisture, and were usually somewhat desiccated. Two or more adult males were often caught together, and in most of these instances the first one caught probably served as bait attracting another and arousing his pugnacious interest. Injuries were frequent, and some deaths occurred because in the close confines of a trap the loser in a fight was unable to escape further attacks.

Most of the skinks caught were examined, and released within a few minutes. Snout-vent length was measured by holding the skink against a rigid transparent plastic millimeter ruler and exerting a slight pull on each end of the lizard until it tired and relaxed its muscles, eliminating bends and kinks. Even with such precaution, precise measurements could not be obtained and the readings often varied a millimeter or more for the same skink measured two or more times on the same day. Tail length was similarly recorded with separate readings for the original and regenerated portions. Also recorded were sex (when discernible), color and pattern, breeding data, injuries, general condition, and sometimes temperature. Many of the skinks were brought to the laboratory, and were weighed to the nearest tenth of a gram.

Occasional trips were made to localities away from the Reservation to collect skinks. Some of those obtained were kept under observation in terraria where their behavior was studied. Most were preserved and were used for data on habitat preferences, seasonal changes in the gonads, size group, stomach contents, and various other items of information.

Description

The scutellation and osteology have been described in detail by Taylor (1936:39-48 and 199-206) and others, and need not be repeated. The five-lined skink is slender and elongate, somewhat snakelike (though much less so than many other skinks) as the head, neck, body, and tail are not well set off from each other, and the sleek, streamlined contours are broken only by the small limbs protruding from the sides of the body. The body is slightly flattened laterally, tending toward quadrangular shape in cross section. The head is wedge-shaped, with a short, rounded snout. The nostrils are laterally placed, well back from the tip of the snout. The eyes are small and deep set; the iris is dark. The neck is thick and strong, nearly as long as the head. The torso is 3½ to 4 times as long as it is wide. The tail is almost square in cross section at its base, but is circular in cross section for most of its length. The limbs are moderately developed; when adpressed along the sides of the body, the forelimb and hind limb overlap by a length about equal to the longest toes of the forelimb. The limbs are pentadactyl and all the toes are well developed and have claws (Figures 1 and 2). The claws are short, and are curved in such a manner that their tips are directed downward, each approximately at right angles to the axis of the toe (Figure 2b). The limbs are moderately thick and muscular. The upper arm and forearm segments are of approximately equal length, as are the femoral and tibio-fibular segments of the hind limb.

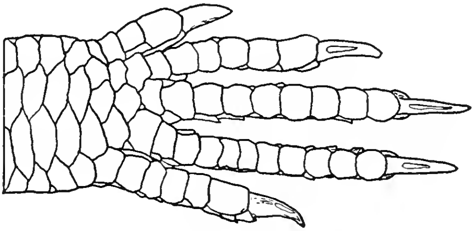

FIG. 1. Antipalmar view of right front foot, × 9.

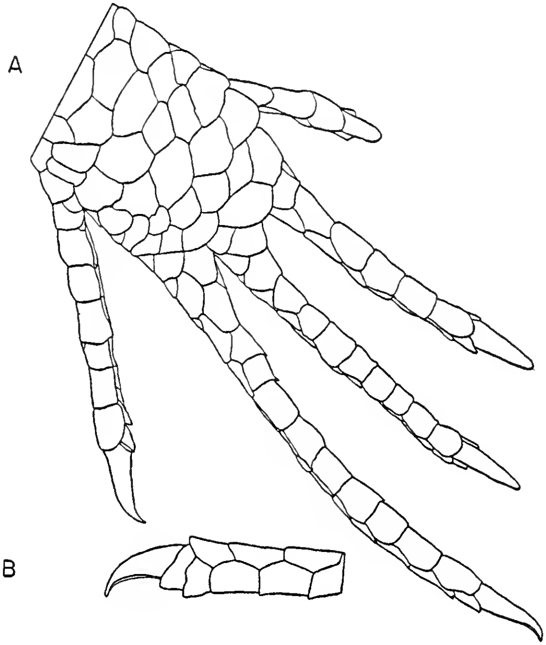

FIG. 2. A. Antiplantar view of right hind foot, × 9.
B. Terminal part of second toe of left hind foot, and its claw, in lateral view, × 9.

The five-lined pattern is characteristic of the hatchling, but gradual ontogenetic change results in its dulling, suppression, and eventual loss. In the hatchling the ground color of the head and body is black or dark brown, with five milky white longitudinal stripes extending the length of the head and body, and on the basal one-fourth of the tail. The five light lines are of approximately equal width, and are separated by dark interspaces 1½ to 2 times as wide. The mid-dorsal stripe includes most of the two mid-dorsal scale rows. Posteriorly it extends onto the base of the tail, where it becomes increasingly suffused with the blue color of the tail, widens, and loses its identity. In the nuchal region, this dorsal stripe narrows and splits into left and right branches, which diverge anteriorly to form a lyrate pattern on the head. On either side of the dorsal stripe are the dark interspaces, nearly twice as wide as the stripe itself and tapering to a point posteriorly on the tail, likewise tapering anteriorly to a point immediately above and in front of the eye. Lateral to these dark areas are the dorsolateral stripes; they extend from the basal one-fourth of the tail anteriorly onto the head along the superciliary region, tapering to a point on the anterior superciliary. Below these stripes are the dark lateral areas which extend from the basal part of the tail anteriorly along the sides of body and neck region (including the upper half of the aperture of the ear), eye region, and loreal region. Below this dark area on each side is the lateral stripe. It extends along the sides just above the level of the limb insertions (broken or pinched to a fraction of its average width above the hind limb insertion), broken by the ear opening, and extending anteriorly to include all the supralabial scales (with the exception of their upper edges) and the rostral. Here the left and right lateral stripes may be said to join; however in the facial region these stripes are not well defined, partly because the dark areas that border their lower edges do not extend so far forward. This lowermost dark area is about equal in width to the lateral stripe. It extends from the posterior infralabials posteriorly, to include the fore- and hind-limbs, and onto the basal part of the tail. The ventral surface of the head and body is dull white or pearly gray.

Thus, there are 12 longitudinal bands of color on the body: the five narrow, subequal, pale lines separated by the six dark areas, of which the dorsal and dorsolateral are broad and of approximately equal width, while the ventrolateral is narrower; and lastly the broad, pale ventral area.

The tail in young individuals is bright blue. In *Eumeces* the tail characteristically has a color different from that of the body, and is usually more conspicuous; in many species it is blue, but in others it may be purple, greenish-blue, red, pink, or orange. Hatchlings have the most brightly colored tails, and as growth proceeds the colors gradually become duller. In *E. fasciatus* the bright colors of the tail are mostly or entirely lost in old adults, especially in males, and in individuals of either sex that have lost their original tails

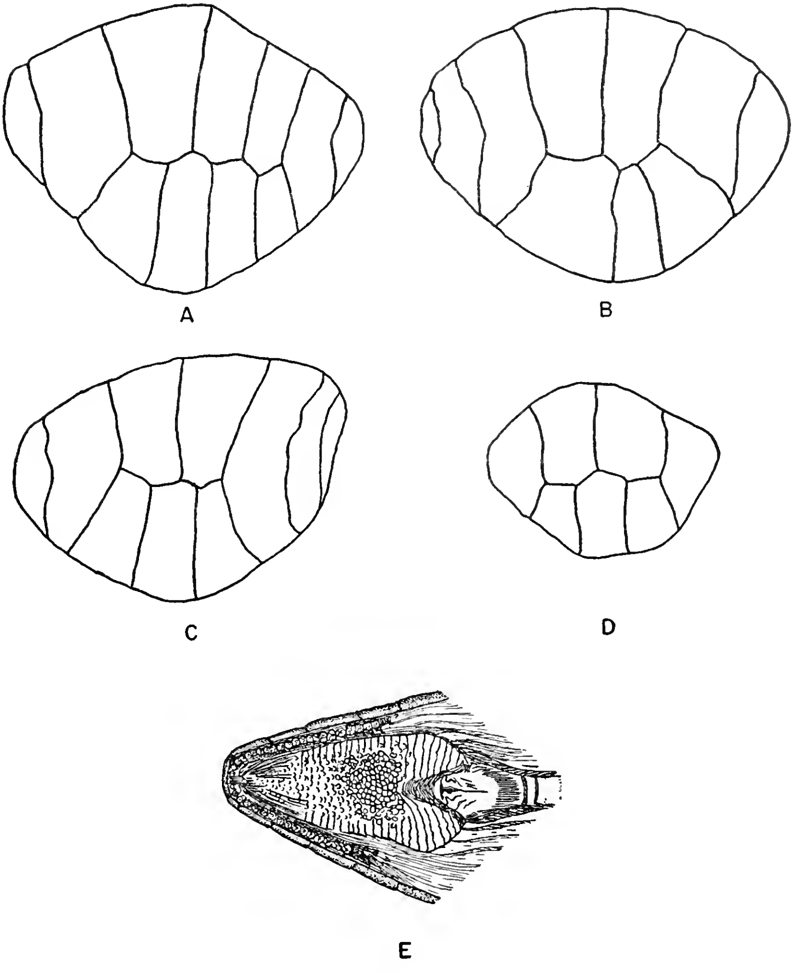

FIG. 3. A. Osteoderm of an old adult male, from near the midline of the back, × 25.
B. Another osteoderm from same male, from belly near midline, × 25.
C. Another osteoderm from side of same male, at a point approximately halfway between foreleg and hind leg, × 25.
D. Osteoderm of a juvenile obtained in April, from near midline of back, × 25.
E. Tongue from dorsal view, shown in its normal position in the lower jaw, × 2½.

and regenerated new tails. Young which lose their tails and regenerate them at an early age have the regenerated portions colored almost as brightly as the originals at first.

The skin is tight fitting and relatively thick, stiffened by a bony armor. A small bony plate or osteoderm underlies each scale. Oliver (1951:127) has called attention to the pattern of ornamentation on the osteoderms, which becomes more complex with advancing age. He has suggested the possibility that age might be accurately determined on the basis of extent of osteodermal ornamentation. I have compared osteodermal ornamentation in marked individuals of known age, but have found it to be of limited applicability as a method of age determination; size and pattern are probably more satisfactory bases for estimating age, even though they do not permit definite aging of old adults and are not infallible for skinks short of adult size. In adult *E. fasciatus* the pattern of ornamentation is closely similar to that figured for *E. laticeps* by Oliver (op. cit.) and also resembles the pattern shown for an Old World skink, *Mabuya multifasciata,* as figured by Smith (1935:2). The pattern differs somewhat in osteoderms on different parts of the body, and is most nearly symmetrical in those near the mid-line on either dorsal or ventral surface (Figure 3).

Relationships

Eumeces is a widespread genus occurring in the New World in southern Canada and southward into Costa Rica. The greatest number of forms is in Mexico. In the Old World numerous species occur in southeastern Asia and on adjacent islands, and other species occur westward across southern Asia, and across North Africa to Morocco, with a major break in the continuity of distribution in the Himalayan region. Taylor in his revision recognized 57 forms with fifty full species, belonging to 15 major groups within the genus. Since then only relatively minor changes in classification have been proposed. Several new species and subspecies have been named, and several species have been relegated to the status of subspecies.

Within the genus there are several groups that have representatives in both the New World and the Old World. Smith and Etheridge (1953:159) point out that the most primitive line of *Eumeces* is best represented in the Old World, where there are two groups and nine species, while in the New World this line has only three tropical relict forms. For this reason, Smith and Etheridge concur with Taylor (1936:67) in considering the genus to be of Old World origin; but the two main lines of the genus (the four-lined and five-lined stocks) are both regarded as being of New World origin. According to this idea, the Asiatic members of these two groups migrated from the New World. In the early Tertiary, warm temperate climates extended north to the Arctic Circle, and *Eumeces*, or at least some of its species, may have had a distribution straddling migration routes to both North America and Asia.

Of the 15 groups within the genus, the *fasciatus* group, with a dozen species, has more representatives than any other. The *fasciatus* group is characterized by having the tail bright blue with dorsal body pattern of five light lines on a darker ground color; mid-dorsal line bifurcating on head to form lyrate markings (this striped pattern and bright color of the tail becoming dull or obsolete in the adults); medial preanal scales overlapped by those lateral to them; two pairs of nuchals; no postfemoral pocket; four supraoculars; scales on sides of body in parallel rows. The characters that separate members of the *fasciatus* group from each other are minor. The width and position of the light lines differ somewhat among them. The mid-dorsal light line bifurcates either on the nuchals or on the parietals. The complex of scales in the temporal region differ in shape and relative size.

The following table, compiled mostly from information set forth by Taylor (1936:186-283), indicates some of the main differences and similarities between species in the chief characters upon which the classification is based.

The close resemblance between *E. fasciatus* and its Asiatic relatives is remarkable considering the great distance separating them and the long time that must have elapsed since their isolation began. Some of the Asiatic forms differ from each other almost as much as they differ from *fasciatus*. Of the Asiatic species, *elegans*, *tamdaoensis*, *oshimensis*, and *marginatus* differ from *fasciatus* in markedly larger size; *elegans*, *marginatus*, *oshimensis*, and *stimsonii* differ in lacking a postnasal; all but *tamdaoensis tunganus* and *xanthi* differ in having only a single postmental; all but *tunganus*, *E. latiscutatus okadae* (and sometimes *oshimensis* and *elegans*) differ in reduced number of scale rows; all but *tunganus* differ in having a lateral postanal scale differentiated, and usually keeled; *tunganus*, *xanthi* and *elegans* differ in having a patch of enlarged scales on the posterior side of the thigh; and in all, the primary temporals and upper and lower secondary temporals differ in size and proportions. Although some of the Asiatic forms seem to be directly derived from others, *fasciatus* is somewhat intermediate

TABLE 1. DISTRIBUTION, PATTERN, SIZE, AND LEPIDOSIS OF THE "FIVE-LINED" SKINKS (FASCIATUS GROUP OF THE GENUS EUMECES)

	fasciatus	*laticeps*	*inexpectatus*	*tunganus*	*xanthi*	*elegans*	*tamdaoensis*	*oshimensis*	*stimsoni*	*barbouri*	*marginatus*	*latiscutatus*
Distribution......	E U.S., except Fla. and N New England	Most of E U.S., except N tier of states	SE U.S.	W Szechwan (in N China)	SE China	SW China, Formosa, Pescadores I.	Indo-China	Amami-gunto I.	Ishigaki-jima, Riu Kiu I.	Amami-shima	Okinawa	Japan, (main I.)
Juvenal Pattern...	5 lined	5 or 7 lined	5 or 7 lined	5 lined	5 lined	5 lined	5 lined	5 lined	7 lined	....	5 lined	5 lined
Max. snout-vent length in mm...	80	130	89	81	76	96	....	99	63	66	93	80
Postnasal.........	present	present	present	present	present	absent	present	absent	absent	present	absent	present
Postmental.......	2	2	2	2	2	1	2	1	1	1	1	1
No. scale rows....	28–30	30–32	30–32	28	22–24	26–28	....	26–28	26	22	26	26 (or 24)
Lateral postanal scales..........	undifferentiated	undifferentiated	undifferentiated	undifferentiated	differentiated	keeled	....	keeled	keeled	....	keeled	keeled
Large scales on back of thigh...	absent	absent	absent	present	present	present irregular	....	absent	enlarged; regular	absent	absent	absent
Median subcaudals.....	widened	widened	not widened	widened	widened	widened	....	widened	not widened	widened	widened	widened

between the more divergent forms, and fulfills most of the conditions to be looked for in an ancestral type.

The American *Eumeces laticeps* and *E. inexpectatus* seem to be more specialized than *E. fasciatus* and might have been derived from it or from a common ancestor differing but little from the modern *fasciatus*. Both differ from *fasciatus* in having more scale rows. *E. laticeps* also differs in having eight instead of seven supralabials and in having the median subcaudal scales greatly widened, in having intercalated plates on the outer side of the fourth toe nearly to the ultimate phalanx, posterior supralabial low and elongate, young sometimes seven-lined instead of five-lined, and especially in much larger size, stocky build, and in early loss of striped pattern. *E. inexpectatus* differs in having the median subcaudals not at all enlarged, and in having the dorsolateral stripes a little more widely separated from the mid-line.

Eumeces fasciatus and its relatives present a curious exception to Jordan's Rule, which states that the nearest relatives of any given species are to be found neither in the same area nor in a remote one, but in an adjacent region separated by a barrier. *E. fasciatus* is absent from almost all of Florida; otherwise its range overlaps most of the ranges of both *laticeps* and *inexpectatus*, the former including the southeastern United States south of about latitude 40°, and the latter being mainly in the Atlantic and Gulf states from Chesapeake Bay into eastern Louisiana. Presumably both of these species began their differentiation as southern populations of an ancestral *fasciatus* and later became isolated from it and continued their differentiation until they overlapped it again as distinct species. The differentiation of *laticeps*, being much greater, presumably took place at an earlier time than did that of *inexpectatus*, and at present it overlaps *fasciatus* more extensively. *E. laticeps* probably diverged to such an extent that competition with *fasciatus* is greatly reduced where the two species occur together.

Since *Eumeces laticeps* was recognized by Taylor as a species distinct from *fasciatus*, numerous authors have accumulated field observations that demonstrate ecological divergence between the two. Conant (1951:33) wrote that in Ohio *laticeps* prefers a dry habitat of bare rocks, cliffs, dry hillsides, and trees. He summed up the habitat difference as follows: "*Fasciatus* appears to be essentially terrestrial, to prefer a moist environment and to be at home in ravines in southern Ohio. *Laticeps* on the other hand, is largely arboreal (particularly adults), prefers dry cliffs, sunny hillsides and hilltops and lives in general above the habitat of *fasciatus*." Netting

(1939:127) likewise states that in Pennsylvania *E. laticeps* inhabits drier places than does *fasciatus,* and is largely arboreal. Other authors with few exceptions agree that *laticeps* is largely arboreal, but most describe it as at home in forest swamps and bottomlands. My own field experience with it is limited. In the Pigeon Lake area of Miami County, Kansas, the northwesternmost known locality of occurrence for *laticeps,* the habitat relations described by Conant for Ohio were almost reversed. *Eumeces laticeps* was relatively scarce, and confined to the vicinity of the swamp chiefly in areas that are flooded in time of high water. All those seen were on or near massive snags of dead trees still standing, but decayed and honeycombed with cavities. Slabs of bark clinging loosely to the tree trunks, with spaces beneath, provided shelter for the skinks and for the abundant arthropod fauna which probably constituted their chief food source. This is one of the few places in Kansas where a remnant of the original bottomland forest remains. In central Louisiana, in 1947 and 1948, persons living on the Kisatchie National Forest told me of large, red-headed skinks living in hollow trees, which must have been *E. laticeps.* In the literature *E. laticeps* is frequently referred to as red-headed, although the reddish suffusion on the head of the adult male is ephemeral in this species as it is in *E. fasciatus* and others. The heightened activity of the adult males in the breeding season seems to have drawn attention to this conspicuous temporary coloration while its absence at other seasons has scarcely been mentioned.

Mansueti (1948:213) describing the habits of *laticeps* in Maryland, Louisiana and elsewhere in the southern states, emphasizes its arboreal habits, referring to it as "'scorpion' of the treetops." He describes it as dashing up and down tree trunks, along fences, and in abandoned buildings. However, he states that it also spends much time on the ground, and may take refuge in holes and cracks near ground level, and gravid females are less arboreal, making their nests in decayed logs of chestnut or oak. He mentions individuals having been found living far above ground in tall trees, in nests of birds of prey. One old male that was frequently seen by him always retreated far up a dead chestnut tree that towered above the surrounding forest of scrub pine. Mansueti also mentions arboreal combats between males and implies that they are territorial. Taylor (1936:59) described *laticeps* as typically an arboreal form, almost invariably found in trees, and he indicated that it has claws more curved than in other species—an obvious arboreal adaptation. Parker (1948:25), however, stated that "*E. laticeps* is reputed to be rather arboreal, but field work in western Tennessee has not borne out this belief. A few of the specimens have been found in tall, dead trees, as has *E. fasciatus*." This statement evidently was based on a small number of observations.

Cook (1943:15) mentions a female *laticeps* found in a nest with a clutch of 27 eggs (hence certainly a communal nest of two or more females) in a burrow under a log, on July 8, 1941, in Lee County, Mississippi. This account is under the name *Eumeces fasciatus* but the large size of the female precludes the possibility of it being either *fasciatus* or *inexpectatus*. The remainder of Cook's account is evidently based on a composite of observations on all three species.

Goin and Goin (1951:29-33) have given an excellent brief account of behavior and seasonal schedule in a small colony of *E. laticeps* near Gainesville, Florida, based on almost daily observations over a period of years. In view of the greatly different climatic conditions, the seasonal schedule is remarkably similar to that of *E. fasciatus* in Kansas, and it seems that the minimum threshold temperatures required for activity are much higher in *laticeps*. Temperatures of 80° F. or above for several consecutive days seemed to be a necessary stimulus for emergence from hibernation; emergence was in the last week in March or the first week in April in Florida. Hatching was found to take place in late June or early July. Adults were last seen before retiring into dormancy in the latter half of September and young of the year remained active into October some two or three weeks later. The skinks observed all lived in hollow water-oaks. When the population was at an especially high level, in the late summer of 1949, each hollow oak was inhabited by one young and one adult. Territoriality and mutual exclusiveness of adults and even of young seems to be implied. The skinks were seen eating spiders, ants, and cockroaches.

Neill (1950:115) mentions one sizable colony of *E. laticeps* living in a treeless urban area, in Georgia and depending for shelter on piles of metal drums and other industrial equipment. Evidently, however, this was an exceptional situation. In another paper, Neill (1948b:109) described the specialized hibernation site requirements of *laticeps* in Georgia; the skink retires inside large, rotting pine stumps, especially those that are leaning. He states (1948a:157) that in Georgia, *laticeps* is most common in the Coastal Plain and is much less numerous above the Fall Line (the line between the Coastal Plain and the Piedmont). Deckert (1918:31) wrote of "*Plestiodon fasciatus*" in the vicinity of Jacksonville, Florida, where only *E. laticeps* and *E. inexpectatus* occur: "Inhabits hollow trees, always near water. Blue-tailed ones often live around human habitations."

With regard to the ecological traits of *E. inexpectatus* that distinguish it from *fasciatus,* authors are much less definite, and evidence is somewhat conflicting as the differences are relatively minor. Engels (1949:269) noted the occurrence of *E. inexpectatus* on two low islands of submarine origin, off the North Carolina Coast, Harkers Island and Shackelford Banks, and he surmised that the absence from them of *E. fasciatus* and *E. laticeps* must have some ecological significance, since all three species occur on the adjacent mainland. Most of the island *inexpectatus* were taken from beneath loose bark of standing trees, while mainland *fasciatus* was taken from beneath loose bark of fallen trees.

Barbour and Carr (1940:129) wrote of *inexpectatus* in the vicinity of Miami, Florida: ". . . it seems to be the only one [of the five-lined skinks] which has adapted itself to life under the rather specialized environmental conditions existing in its rocky and decidedly tropical habitat. It is one of the very few forms which have established themselves on some of the waterless and poorly vegetated islands on both coasts of the peninsula. *E. inexpectatus* is much less arboreal than either *laticeps* or *fasciatus.* Although it climbs trees when pressed, it is usually found on the ground among leaves or about fallen logs, and particularly about stone walls or old buildings made of cut rock."

On the other hand, Neill (1948a:157) states that in Georgia, *inexpectatus* is often observed basking on tree trunks, and though adults often forage on the ground, they dash for the nearest tree when disturbed, usually climbing to a considerable height before halting. The juveniles, however, are said to climb only rarely; they hide beneath objects on the ground when they are pursued. Neill stated that *E. inexpectatus* occurs in dry pine forests where *laticeps* and *fasciatus* are lacking, as well as in moist or even swampy woods. *E. inexpectatus* often forages on the sides of old buildings.

Hoffman (1953:172), in discussing means of differentiating between *inexpectatus* and *fasciatus* in Virginia, states that there are ample differences in color and behavior as well as in scalation. He describes the color difference (blue color of tail of juveniles extending anteriorly beyond pelvis; light stripes reddish-orange on head, sublateral line present, in *inexpectatus*) but he does not describe the differences in behavior. He states that *inexpectatus* is the most abundant lizard in southeastern Virginia. Carr (1940:76) also states that *inexpectatus* is less arboreal than *laticeps* and is often found under logs and boards in dry sand.

E. inexpectatus thus seems to be adapted to a somewhat drier, more open, habitat than that typical of *fasciatus*, but it is not clear whether either species is more arboreal in habits. It is to be hoped that the present inconclusive summary will draw attention to the problem and will lead to more critical comparisons of the habitats and behavior of the two species by herpetologists in the southeastern states. The differences, both ecological and morphological, that distinguish *inexpectatus* from *fasciatus* are of a degree usually found between subspecies of the same species. The extensive geographic overlap between them is indeed remarkable in view of the slight degree of differentiation, morphologically and ecologically. They are, however, complementary in part in their ranges, while *laticeps* shares all parts of its range with either one or the other, or both of them (see Figures 4 and 5).

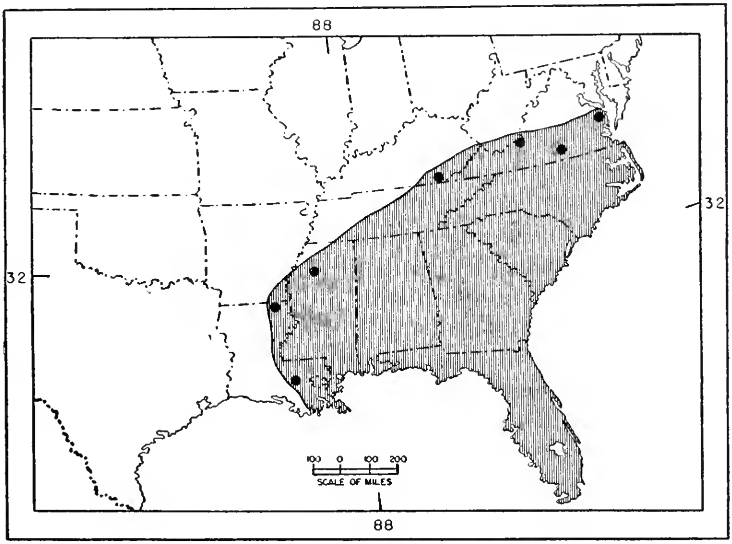

Fig. 4. Geographic distribution of *Eumeces inexpectatus*, as indicated by published records; only marginal and near-marginal records are shown, excluding those of doubtful validity.

Under present conditions, with these three species so similar in habits and so extensively overlapping in geographic range, it is difficult to visualize a barrier such as would have been required for allopatric speciation of the type, usual in vertebrates, to have occurred. One might be tempted to postulate sympatric speciation, with the parent form, presumably *fasciatus*, giving rise to the other two by abrupt mutations. However, the demonstrable antiquity of the five-lined skinks would allow ample time for divergence, allopatric speciation, and subsequent disappearance of the barrier and intermingling of populations. The displacement of floras and faunas that occurred in the Pleistocene, with the successive advances and retreats of the continental ice sheets might have had some part in bringing about the present overlapping distribution, after the disappearance of the original barrier. Such a barrier might have been an eastward extension of the central grasslands to the Atlantic Coast at a time when the climate of the continent was warmer and drier.

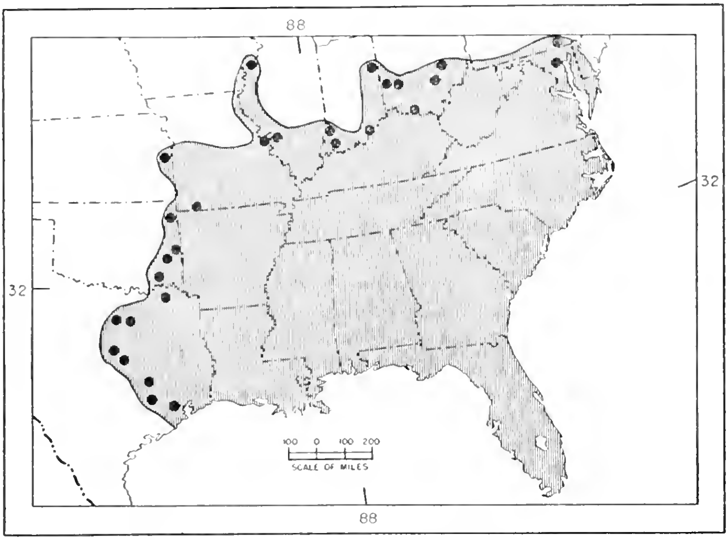

FIG. 5. Geographic distribution of *Eumeces laticeps,* as indicated by published records; only marginal and near-marginal records are shown, excluding those of doubtful validity.

Habitat and Limiting Factors

TEMPERATURE AND MOISTURE RELATIONS

For approximately half the year, at the latitude of northeastern Kansas, five-lined skinks are dormant. In early fall, even before the advent of cold weather, they are hard to find apparently having begun their retirement into the sheltered situations where they spend the winter, even though they may not be fully dormant at that time.

Remarkably little is known of the hibernation habits of this species or of reptiles in general for that matter. The limit of tolerance to low temperatures, the type of insulating medium, the moisture relationships, the specific stimuli which cause the animal to retire to its hibernation site or to emerge from it have not been determined. On only a few occasions have natural hibernating sites or the dormant skinks in them been observed by zoologists. Linsdale (1927: 78) recorded one found in a sawdust pile late in the winter of 1924 in Doniphan County, Kansas. Hamilton (1948: 211) found skinks of this species hibernating in Grant Parish, Louisiana, in hollow logs 18-20 inches in diameter, five in one log and three in another, on January 23, 1943. Frost in the damp wood almost reached the lizards, which were in a torpid condition. These observations were made when the temperature was 36°F. after the weather had begun to moderate following an unprecedented four-day cold wave when temperatures dropped to within a few degrees of 0°F. In both logs the skinks were accompanied by hibernating anoles (*Anolis carolinensis*). Neill (1948b:109) in Richmond County, Georgia, found *E. fasciatus* hibernating in old stumps, fallen timber, piles of debris, or beneath rocks and ground litter. Beneath scraps of rotting wood he often found dead, frost-rimmed specimens which apparently had frozen to death. Hibernating skinks of this species were found singly or in pairs. Some were not fully dormant when found but could only gape and twist when uncovered.

Of hibernating *E. laticeps,* Neill wrote, "Many examples are covered with a waxy exudation, which I believe to be a secretion of the lizard itself, rather than of the surrounding medium. This exudation has been noted in other species also." Scott and Sheldahl (1937:192) described a hibernating aggregation of *Eumeces septentrionalis* found in Palo Alto County, Iowa, on February 15, 1937, as follows: "The skinks were found beneath a ledge of yellow clay about four and one-half feet below the surface. The lizards, 52 in number, were assembled in a compact group about the size and shape of a football. A soft, web-like material surrounded the mass and adhered to the bodies of the animals. Upon being uncovered some of them exhibited signs of life; others were dead." Breckenridge (1943:595) reported that a gravel digging crew found hibernating *E. septentrionalis* in late October and in January at depths of two feet (one), and three feet (groups of three and eight). Tihen (1937:405) recorded that two five-lined skinks found on January 13, 1948, were hibernating eight feet underground at Ranson, Ness County, Kansas. This locality is far to the west of the main range of *fasciatus*. Conant (1951:30) mentions the finding in Ohio of a young blue-tailed skink under a log where it seemed to be hibernating, on January 22. The spot where it was resting was soggy, and surrounding areas were covered with several inches of water.

In the course of the present study, no five-lined skinks were found hibernating under natural conditions, but on numerous occasions in early spring, two or three or four skinks were found together under massive flat rocks in semi-torpid condition, beside deep holes or crevices which presumably led to their hibernation sites in better insulated cavities. In the winter none could be found in such situations under large rocks, nor in the superficial types of hibernation sites described by Neill and Hamilton in the southern states. In the more severe winter climate of Kansas better protected hibernation sites are required. In the rock ledge situations where skinks were studied, excavation for the purpose of finding hibernating individuals was not practical.

On several occasions when skinks were put in the freezing compartment of a refrigerator and frozen solid, at temperatures several degrees below freezing, they failed to revive when warmed. However, they can survive temperatures a little below freezing. On April 1, 1953, one was placed in the freezing compartment with a thermometer inserted rectally. After 2½ hours when the compartment was opened, this thermometer showed a temperature of —2.5°C, after a delay of several seconds in obtaining a reading because of condensed moisture on the thermometer obscuring the mercury column. Another thermometer that rested beside the skink in the compartment showed 27°F. The skink was limp and immobile. It was placed on a table top at normal room temperature, and it warmed rapidly. When it had reached 1.5°C, it contracted its muscles in response to a light pinch. At 9.5°C it raised its head and had its eyes partly open. Twenty minutes after its removal from the freezing compartment, it was still lying in the same position, its temperature having reached 13.5°C. When handled it seemed dazed for several seconds as if just awaking. Then it crawled away briskly.

On March 28, 1953, a skink was placed in the freezing compartment for about 10 minutes, and upon removal its temperature was recorded as —.5°C. It was not frozen, but was limp and unresponsive to such stimuli as pinching or pricking. At 1.5°C feeble movements of the legs were noticed. The eyes were still closed. At 3.4°C the legs moved as if in walking. At 6.0°C the skink raised its head and took several steps forward. At 7.5°C it protruded its tongue and dragged itself about for several steps. At 9.0°C movements of the sides indicated an inspiration approximately every three seconds. At 12.2°C it opened its eyes.

On March 25, 1953, a skink that I had caught the day before and left overnight in an unheated room, was found to have burrowed into loose earth in its container. When exposed, its temperature was 1.8°C and it was unable to crawl normally, but took only one step at a time, and progressed with slow lateral squirming motions. Placed on the ground outside the building, in the shade where there was still a little frost, it moved forward persistently for several inches trying to burrow into the surface litter. After a few minutes, its eyes were shut and it seemed incapable of further locomotion. Its temperature was 1.4°C. When placed on its back it was able to turn over slowly after several seconds. A few minutes later its temperature was 0°C, and it was totally helpless, although still capable of feeble movement. When stimulated by touch, it flexed its body a little, or moved each limb slowly in an arc as if walking, the movement taking several seconds. Placed on its back or side it was unable to right itself.

Less than three hours later I saw a skink that was active in the field. Slight movement at the edge of a rock that was exposed to sunshine attracted my attention and turning the rock I found the skink underneath, lively enough to scramble for shelter but slow and stiff compared to those that are fully active. Its temperature was 13.5°C and air temperature was 7.5°C. In damp soil beneath the rock where the lizard was found, temperature was only 5.7°C. It seemed that the skink had been sufficiently warmed by contact with the undersurface of the rock to move into the open, and was just emerging when I approached. After capturing the skink, I set it on a rock in the sunshine, and in five minutes its temperature had risen to 26°C.

As compared with its reptilian associates in northeastern Kansas, *Eumeces fasciatus* is outstanding in its ability to become active and carry on normal activities at relatively low air temperatures. In spring it is usually seen in the open before any other kind of reptile, because it has the capacity to move about sluggishly at temperatures so low that some other reptiles are numbed and completely immobilized, and because it has small size enabling it to make rapid adjustment upward by insolation, or contact with sunshine-warmed surfaces. By virtue of this ability it has been able to extend its range farther northward than most other reptiles, and it has gained the advantage of a longer growing season. This advantage was especially apparent in the spring of 1953. A mid-March warm spell with seven out of eight successive days having maximum temperatures in the sixties culminated on March 20, with a maximum air temperature of 82°F. This warmth was sufficient to activate most of the five-lined skinks, and a few reptiles of other kinds. After the unseasonably high temperature of March 20, there was rapid return to cooler weather with temperatures frequently below normal throughout April. As a result there was little activity of other kinds of reptiles that month, but five-lined skinks were active on most days. On only a few days, those with temperatures in the low forties or those on which the sky remained overcast, did the skinks remain inactive. On most days maximum temperatures were in the fifties and sky was clear. Under these conditions the skinks were able to emerge and bask, rapidly raising their body temperatures far above those of the air and substrate.

By the end of April some kinds of deciduous trees have not yet begun to leaf out, and in most other kinds the leaves are still in an early stage of development. Absence of a leaf canopy during April permits the skinks to utilize the spring sunshine to maintain their body temperatures at almost the same high level that they maintain in the same situations in hot summer weather.

TABLE 2. TEMPERATURES (IN DEGREES CENTIGRADE) OF SKINKS FOUND UNDER FLAT ROCKS EXPOSED TO SUNSHINE, CONTRASTED WITH AIR TEMPERATURES; SPRING OF 1953.

Date	Age and sex	Skink temperature	Air temperature
March 23	Ad. ♀	20.8	12.4
March 23	young	24.7	12.4
March 25	Ad. ♂	22.8	12.5
March 25	young	21.0	12.5
March 25	young	25.7	14.5
March 25	young	22.5	14.5
March 27	Ad. ♂	26.6	16.5
March 27	young	22.0	16.5
March 27	Ad. ♀	22.5	16.5
March 27	Ad. ♀	20.5	16.2
March 27	Ad. ♀	26.5	19.3
March 27	Ad. ♀	30.7	19.3
April 4	young	22.0	18.1
April 5	Ad. ♀	26.0	13.0
April 6	Ad. ♂	31.5	13.5
April 6	Ad. ♂	23.7	16.0
April 6	Ad. ♀	22.2	16.0
April 6	Ad. ♂	20.0	16.0
April 6	Ad. ♀	20.0	16.0
April 6	Ad. ♀	26.5	20.3
April 20	Ad. ♀	29.7	17.2
April 20	Ad. ♀	25.8	17.2

Recent studies by Cowles and Bogert (1944:288-289) and Bogert (1949:198) have brought out the fact that terrestrial poikilotherms, and especially lizards, maintain fairly high and constant body temperatures through behavioral thermoregulation, during their periods of activity. For genera and species of lizards, there are optimum body temperatures, which the individual tends to maintain, fluctuating within a range of only a few degrees while it is active. Forms that are not closely related may differ notably in their optimum temperatures, although within any one genus the range is slight. For example in the iguanid genus, *Sceloporus,* Bogert found that different species from such distant regions as Arizona and Florida agreed in having body temperatures approximating 35° or 36° C., while different members of the teiid genus *Cnemidophorus* in the same two regions were found to approximate 41° C. in mean temperatures. In commenting on the distribution of North American lizards as affected by opportunity for behavioral thermoregulation by direct insolation, Bogert (*op. cit.*:205) wrote: "Such secretive lizards as skinks (principally *Eumeces* in North America) with low body temperature preferences approximating 30° C. are dominant in Florida and the Gulf Coast, in contrast to the Teiidae and Iguanidae (several genera in the United States), which are far more abundant in the arid regions of the Southwest." Bogert and Cowles (1947: 19) record that in a large individual of *Eumeces inexpectatus* taken near the Archbold Biological Station in Florida, the body temperature was 33.2° C.

In the 1952 season, a small thermometer of the type described by Bogert (*op. cit.*:197) was frequently carried on collecting trips, and cloacal temperatures were recorded for the lizards collected. For those found in traps the opportunity for behavioral thermoregulation was limited, and temperatures usually approximated those of the air. The circumstances of capture, and the air temperatures were recorded for most of the skinks taken. For those found under rocks or in other shelter, the temperature usually approximated that of the immediate surroundings, and averaged much lower than for those taken in the open, but some found in such shelters had temperatures many degrees higher than their surroundings, and were fully active, having evidently just taken to cover to escape notice as the collector approached. As soon as a lizard was secured it was held in a leather glove or heavy cloth to prevent conduction of heat from the collector's hand, and a reading was taken within a few seconds. Most of the skinks found in the open could not be caught immediately but were secured only after minutes of maneuvering on the part of both collector and lizard. In most instances this maneuvering probably entailed some loss of heat by the lizard, as it interrupted its thermoregulatory behavior to run to a place of concealment, usually in shadow on a tree trunk, or in or beneath ground litter. Excluding all those not found active in the open, the mean temperature, in a sample of 41, was 31.5° C. ± .60. This figure is thought to be slightly too low because of heat loss by many of the skinks in the time required to capture them.

In order to test the range of tolerance and verify the preferred optimum temperature of the five-lined skink, an experimental terrarium was set up providing extremes of temperature at each end. A false floor of ⅛ inch wire screen was provided, with a seven-inch strip of galvanized sheet metal beneath it at each end. Beneath the screen and sheet metal at one end the space was filled with chopped ice, and "dry ice." Observations were made on hot, clear summer days, with the terrarium arranged so that the half of it containing ice, was in shadow, and the other half was in sunshine. The strip of metal, warmed by direct sunlight, became uncomfortably hot to the touch while at the other end the sheet metal and overlying screen were cooled by the ice. A narrow zone across the middle of the terrarium had screen but no underlying sheet metal and was the only part within which the lizard could maintain normal temperature, one end being uncomfortably hot and the other end too cool. A large dead skink left on the metal strip in direct sunlight for five minutes had a cloacal temperature of 45.3° C., and after five minutes on the screen at the cool end, its temperature had dropped to 25.5° C. On several occasions a number of skinks were put in the terrarium and their temperatures taken at brief intervals. Temperatures ranged from 21.6° C. to 37.7° C. but were mostly within a much narrower range, from 28° to 36° C. One skink that seemed to be sick was sluggish in behavior, not responding to the extremes of temperatures as readily as the other individuals and his temperature fluctuated widely and irregularly. Eliminating this individual, 66 temperature readings taken, from five other skinks, gave a mean of 32.6° C. ± .235. While nearly all the temperature readings were within a range of ten degrees, two of the readings were outstandingly low and perhaps should be discarded. If this is done, a mean of 33.8° C. ± .19 is obtained for the remaining 64. There is distinct bimodality in this series however, with a mean of 34.2° for the 49 higher readings, and a mean of 28.8° C. for the 15 lower temperatures. A similar bimodality is evident in the readings obtained from skinks caught in the open under natural conditions. It seems that the lower readings result from lags in the skinks' response when body temperature drops slightly below the optimum. The skink is quick to make adjustment whenever its temperature appreciably exceeds this optimum level, and is in extreme discomfort at only a few degrees higher temperature. At slightly lower temperatures, however, the skink experiences no discomfort, and only slightly decreased efficiency in its various functions, and its thermoregulatory behavior in making readjustment toward the optimum is likely to be leisurely and interrupted unless its temperature drops below 28° C.

Catching the skinks in the experimental terrarium at frequent intervals to take their temperatures involved some disturbance to them, interrupting their thermoregulatory behavior. The experimenter's first attempt to grasp a skink sometimes failed, and it then dashed about the terrarium for several seconds, probably altering its temperature somewhat. Nevertheless most of the lizards' movements were motivated by thermoregulation. This was especially evident when they were left undisturbed, and is illustrated by the following notes on behavior of an adult female and half-grown young of *fasciatus* and a young *E. obsoletus* on the afternoon of July 21, 1952.

2:58 All resting over cooled metal.

3:01 Female runs to line of sunshine and shadow, coming to rest with approximately half her body in sunshine, the other half in shadow over the cooled metal.

3:03 Female reverses position so that hindquarters previously in shadow are now in sunshine, and forequarters are in shadow.

3:03½ Young runs to middle coming to rest in sunshine on screen.

3:04 Female moves back to the cool end.

3:05 Young moves to edge of cooled metal but not over it, in a narrow middle strip that has sunshine.

3:05½ *E. obsoletus* moves from cool end to middle, partly in sunshine.

3:07 *E. obsoletus* adjusts its position in narrow middle strip of shadow just off the cold end.

3:08 Boards used for shading adjusted back slightly so that *E. obsoletus* is in sunshine.

3:08½ *E. obsoletus* moves back to cold end.

3:10 Young still at middle, but resting mainly over cooled metal with tail partly in sunshine.

3:10½ Young moves out into sunshine at middle.

3:11 Female moves out into sunshine at middle. *E. obsoletus* moves over cooled metal to its edge, coming to rest partly in sunshine.

3:12 Female moves back over cooled metal.

3:13½ Air temperature 33.3°C. *E. obsoletus* shifts a short distance so that it is resting entirely over the cooled metal, with only part of its tail receiving sunshine.

3:17 Young moves about in sunshine, then comes to rest in shadow with half its body over cooled metal.

3:19 Young shifts so that more than half its body is in sunlight in middle section.

3:20 Young shifts away from sunlight, coming to rest with most of its body over the cooled metal.

3:21½ Female moves from cooled metal to sunshine in middle strip.

3:23 Female moves out of sunshine, partly over edge of cooled metal.

3:30 Young moves off cooled metal, coming to rest over edge of warmed metal in narrow middle strip that is in shadow.

3:30½ Young moves back away from warmed metal, pauses briefly, and then moves over cooled metal coming to rest there.

3:31 Female shifts so that about half her body is in sunshine in the middle.

3:32 Female shifts back into shadow, partly over cooled metal.

3:33 Boards providing shade readjusted so that female is in sunshine.

3:33½ Female moves back into shadow over cooled metal.

3:38 Female moves to edge of cooled metal, resting partly in sunshine; sky is becoming slightly overcast.

3:40 Temperature of female 33.4°C.

3:41 Temperature of young 32.8°C.

3:43 Temperature of *E. obsoletus* 32.4°C.

3:45 Young moves to shaded edge of warmed metal. Finds a dead spider dropped there and eats it.

3:47 Temperature of female 32.3°C.

3:48 Temperature of young 36.4°C.

3:50 Temperature of *E. obsoletus* 33.8°C.

3:52 Sky partly overcast with thin layer of clouds; observations concluded.

Having once emerged from its hiding place a skink becomes more or less independent of the temperature of the air and substrate, as it is capable of thermoregulation through insolation. However, after a period of cooling and inactivity in dormancy, or merely resting for the night in temporary shelter, the skink is dependent on warmth from the air or substrate or both to become sufficiently activated so that it can emerge and take advantage of direct sunlight. About 10:00 a. m. on April 13, 1951, when the air temperature was a little less than 10°C., a large adult male rustling among dry leaves attracted my attention. Obviously recently emerged from hibernation, he was caked with dried mud and his eyelids were nearly sealed shut. He had been sunning, however, and was active enough to elude my attempts to catch him, as he scurried into a deep crevice under the ledge. On the morning of March 24, 1951, while the temperature was still between 10° and 15°C., a subadult skink, the first one of the season, was seen sunning itself at the entrance of a deep crevice under the ledge. This skink was still not fully active, and its movements were stiff, yet it was alert and wary, and it quickly retreated back into the crevice. During the first week of May, 1952, skinks were active in abundance and numbers were caught daily in funnel traps and pitfalls. On May 9, however, the maximum air temperature was 16.5°C. with cloudy sky and occasional showers. Under these conditions skinks stayed under cover; none was seen in the open nor caught in a trap, and several found under rocks were slow and sluggish. On May 10 a terrarium with several adults was placed in dilute sunshine beside a window in an unheated room. After a period of basking the skinks were stimulated to activity, but were unable to attain normally high temperatures, and as a result their movements were like slow motion caricatures of the normal behavior. Males approached each other with menacing demeanor, with heads turned, snouts depressed, and forequarters standing high. Frequently one would edge up to another and bite hard at its flanks. The several males were sexually aroused by the presence of the two females, but were capable of only the preliminary phases of courtship, in delayed and protracted form. The temperature of one was 18.2°C. when the sun had nearly set and activity was tapering off, at an air temperature of 16.2°C. At 16°C. skinks in a terrarium with no access to sunshine for the most part showed no interest in food and kept out of sight under cover. When exposed their activity was directed almost entirely toward burrowing into the substrate or searching for objects beneath which to hide. One adult female was partly exposed by scraping away loose soil into which she had burrowed. A mealworm was then dropped just in front of her head. She tested it several times with her tongue and then ate it without emerging, her movements being much less brisk than they normally are in feeding. Probably this approximates the threshhold temperature for feeding behavior. At 19.5°C. the several skinks in this terrarium were moving about in the open although they were not exposed to sunshine, and they accepted food avidly when it was offered, but were much slower than at optimum temperatures. On May 16, 1951, when a pair of skinks were put together in a terrarium in the laboratory at 21°C., copulation ensued but it was of longer duration than in other observed instances, seemingly because of the relatively low temperature.

Relatively few temperature readings on gravid or brooding females under natural conditions were obtained as they were easily disturbed and tended to desert their nests at slight provocation.

To avoid desertions handling was kept to a minimum. Occasionally gravid females were caught in the open, but most of them were in nest burrows under flat rocks. These females found in nests were mostly cold to the touch, and the temperature readings taken on some of them usually approximated the air temperature, being either higher or lower (depending on whether the air was cooling or warming and whether the lizards were warmed by contact with rock or soil receiving sunshine). On May 23, 1952, 22 skinks were seen, four adult males, seven adult gravid females, and 11 young. Of these the adult females all were in nest burrows, and were cold and slow; consequently all of them were caught without difficulty. The males and young, however, were either fully warmed or warm enough to escape rapidly, so that only three of the young and no adult males were caught. Temperatures of the females tested were 25.6°, 23.6°, 23.5°, 22.3°, and 19.4°, and for the three young, 32.8°, 28.4°, and 28.4°. Air temperature varied from 20.5° to 24.8°. For the total of 30 females in nest burrows whose temperatures were taken in 1952, the average was 26.3°C., ranging from 16° to 34°. Gravid females, and those with nests and eggs were rarely seen in the open.

The five-lined skink is confined to a region where summer rains are frequent. It is evident that a regular supply of drinking water is one of the most critical ecological requirements. Bogert and Cowles (1947:19) found that an *E. inexpectatus* experimentally kept at high temperature lost moisture at a more rapid rate than any other reptile tested (including two other kinds of lizards, four kinds of turtles, an alligator, and three kinds of snakes). They remarked that this rapid moisture loss presumably accounts for the inability of skinks to survive in containers when no moisture is readily available, and also accounts for their absence in truly arid habitats. The Natural History Reservation is situated near the western edge of the species' range in a climate that may be near the limit of its range of tolerance. However, on most summer mornings low woodland vegetation is copiously laden with dew, and this evidently fulfills the need for drinking water. Diminution of surface activity and retirement to underground retreats seem to be closely correlated with cessation of rains in late summer. After rainless periods in August and September, when morning dew is no longer available these skinks, especially the adults, are no longer regularly seen in the open. They have retreated to underground shelters where they spend nearly all their time. The time of disappearance varies from year to year and the correlation with varying weather conditions seems obvious. While no actual experiments were performed to determine the moisture requirements, it is evident that the need for moisture rises sharply with increased temperature. Skinks that are dormant in hibernation survive for periods of months without drinking, with but little loss of weight. In their underground shelters temperature is low and presumably relative humidity is high. At temperatures above their optimum of approximately 34°C. the skinks are especially subject to rapid moisture loss, since evaporation of body moisture is resorted to as a device to keep the temperature below the lethal level. The skinks subjected to extremes of temperature in an experimental terrarium were seen to lap up condensed moisture on the cooled metal plate at intervals of a few minutes. After an hour or more in the experimental terrarium they seemed somewhat debilitated. Skinks brought from the study areas to the laboratory for weighing and other records, were ordinarily returned on the following day. When circumstances prevented adherence to this schedule in hot summer weather, mortality could be expected in the skinks kept in cloth bags or glass containers, unless water was provided. Dramatic weight loss of up to more than 30 per cent was recorded in some individuals, kept at the high temperatures which usually prevailed in the laboratory, over periods of days in the summer. Skinks having access to drinking water often ingest amounts far beyond their immediate requirements, which may be stored in the bladder and drawn upon over periods of days as it is needed, or may be utilized to dampen the soil of the underground shelter and raise the humidity, as incubating females seem to do.

GEOGRAPHIC RANGE AND THE DECIDUOUS FOREST HABITAT

Eumeces fasciatus corresponds in its distribution with the original hardwood forests of eastern North America, as mapped by Braun (1950:cover folder) and the "Oak-Wild Turkey Biome" of Shelford (1945:240). Few species of vertebrate animals have ranges that coincide more closely with this extensive area (exclusive of the northern edge, that part characterized by Braun as the Hemlock-White Pine-Northern Hardwoods). This latter is a mixed forest which actually is transitional between the more typical deciduous forest farther south and the Taiga Biome (or Formation) to the north, which is dominated entirely by conifers. At the northern edge of its range *Eumeces fasciatus* is much less generally distributed than it is farther south. Although it is well established and even may be locally numerous in South Dakota, Minnesota, Wisconsin, northern Michigan, Ontario, northern New York, and Connecticut, the locality records from these states are few, and seemingly represent isolated and widely separated colonies that are able to persist because of favorable combinations of environmental factors not of general occurrence in the surrounding regions. Figure 6 shows the extent of the hardwood forests as mapped by Braun (excluding the transitional Hemlock-White Pine-Northern Hardwoods Association) with specific locality records of *E. fasciatus* included in all outlying portions of the range. The locality records are those published by Taylor (1936:206-212) supplemented by other marginal records, more recently published, by Hamilton (1947:64) for New York, Breckenridge (1944:97) for Minnesota, Hudson (1942:42) for Nebraska, Smith (1950:185) for Kansas, Brown (1950:116) for Texas, Neill (1948:156) for Georgia, and Neill and Allen (1950:156) for Florida. Along the northern edge of its range, the skink invades the Hemlock-White Pine-Northern Hardwoods Association, in Massachusetts, New York, Pennsylvania, Ontario, Michigan, and Wisconsin, but does not penetrate far into it anywhere. Correspondence of its northern limits with those of the Oak-Chestnut, Maple-Basswood, Beech-Maple and Oak-Hickory associations is remarkably close, considering the fact that the boundaries of these climax associations are not sharply defined; rather they merge by gradual stages into the northern coniferous forests, with outlying peninsulas and islands where conditions are favorable.

The outlying northern localities where *E. fasciatus* occurs within the Hemlock-White Pine-Northern Hardwoods Association are all within the region of Pleistocene glaciation, which 20,000 years ago, or even more recently, were covered with the continental ice mass during Wisconsinan time. Yet the localized northern populations of skinks evidently are relicts from a time when favorable conditions were more widespread in the general region. Braun (*op. cit.*: 464-465) indicates five successive postglacial stages in the trends of climate up to the present, as revealed by bog pollen profiles: (1) Cool and moist; (2) warm and dry; (3) warm and humid; (4) warm and dry; (5) cool and moist. Stages 2 and 4 would have been most favorable for encroachment of the skink into glaciated regions, whereas stages 3 and 5 might have caused retrenchment of its populations. In view of the localized habits of individuals, and the lack of any mechanism for rapid dispersal, the time available seems no more than adequate for the distance of 200 miles or more northward that the skinks must have moved since the final retreat of the ice sheet. This northward movement involved crossing of formidable barriers such as the Great Lakes. Even minor barriers such as small rivers and creeks, might be expected to halt population movements for long periods.

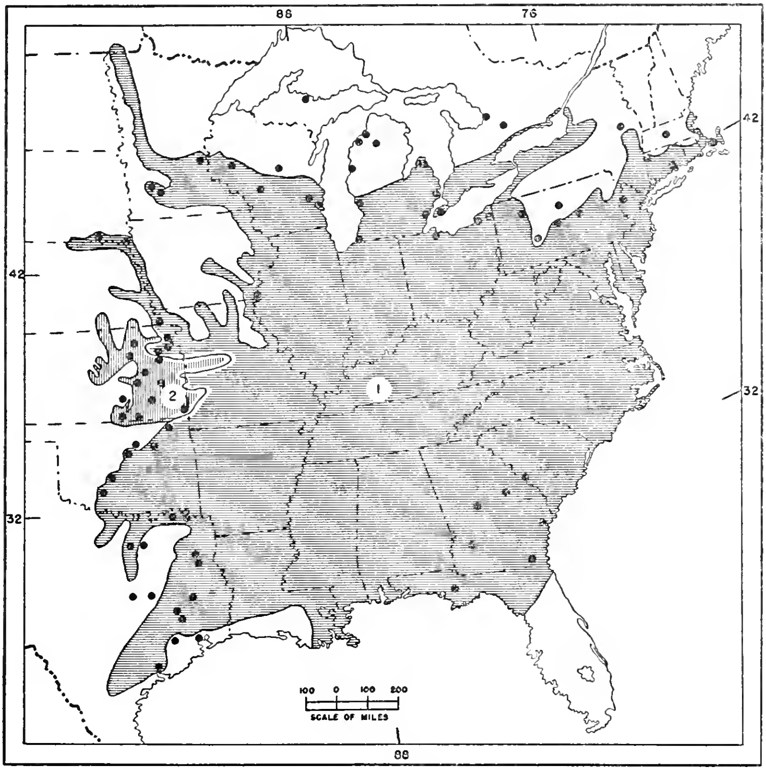

FIG. 6. Geographic distribution of *Eumeces fasciatus* as indicated by published records (marginal and near-marginal records shown, excluding those of doubtful validity). (1) Distribution of the Deciduous Forest Formation of eastern North America, as mapped by Braun (1950), but excluding the Hemlock-White Pine-Northern Hardwoods Association that is transitional to the more northern coniferous forests. (2) The shaded area in Kansas that is outside the Deciduous Forest Formation comprises the Kaw River District, Cherokee Prairie District, and southern Osage Savannah Biotic District (Cockrum, 1952).

The over-all geographic range is approximately square, roughly a thousand miles across, from north to south and from east to west. On the east and south it is limited by the Atlantic Ocean and the Gulf of Mexico. On the north and west its limits correspond with those of the hardwood forests. On the northwest, it reaches southwestern Minnesota and the southeastern corner of South Dakota, extending far out into peninsular extensions of the Oak-Hickory Association which penetrate westward into the prairies along the main river valleys.

In Kansas it occurs over the eastern one-fourth, west to the Flint Hills, and a little farther west in peninsular extensions of the forest along some of the main river valleys. In Braun's map the Deciduous Forest Biome is shown to reach only the eastern edge of Kansas along the Kaw River and Missouri River at and near their junction, the Osage (or Marais des Cygnes) River valley near the Missouri border, and the southeastern corner of Kansas. However, for almost 100 miles farther west from the Missouri border, the country has the aspect of a savannah with scattered groves of trees on hillsides and along streams, providing suitable habitat. The distribution of the five-lined skink in eastern Kansas corresponds well with certain "Biotic Districts" as mapped by Cockrum (1952:12), namely the Kaw River, Osage Savannah (southern part), and Cherokee Prairie. Conversely the skink is excluded from the Short Grass Plains and Mixed Grass Plains Biotic Districts which occupy nearly all of the western three-fourths of the state. There are two specimens in the University of Kansas Natural History Museum, labelled Ranson, Ness County. This locality, in the western third of the state, more than 150 miles from any other recorded station, may represent an isolated colony; however Smith (1950:185) states that the record needs verification, and it is not included in the map, Figure 6.

In Oklahoma the distribution records fit fairly well the portion of the state mapped by Braun as the Oak-Hickory Association of the Deciduous Forest, but extends a little farther west in the northeastern part of the state. A game type map published by the Oklahoma Game and Fish Department, Division of Wildlife Restoration, in 1943 shows in more detail distribution of the main vegetation types within the state. The locality records for the skink fall almost entirely within three of the fifteen vegetation types mapped, namely, the oak-pine, and oak-hickory forest of the state's eastern edge and the post oak-blackjack oak type of the eastern and central parts. The locality records extend almost throughout the area occupied by these three types but not in attenuate westward extensions of the post oak-blackjack type that occur along several of the main stream courses. In Texas likewise the recorded localities fall mainly within the area mapped as deciduous forest, but with several slightly beyond its boundaries. In a detailed map of the "game regions" of Texas (Anonymous, 1945:1), some of these outlying localities fall into the coastal prairie area, and the remainder into the post oak and blackland prairie belts, which grade into each other and the oak-hickory forest.

The former distribution of the five-lined skink may be postulated on the basis of the fossil record of its community associates since it is a primitive and conservative type. Taylor (1936:56) explained the present discontinuous distribution of the genus on opposite sides of the world on the basis of a former northern connection of the continents. He wrote: "I regard migration from North America to Asia as having taken place via land bridges joining the Alaskan peninsula with Asia either at Bering Straits or via the Aleutian Island arc to Kamchatka, or both. One would need postulate but slight climatic changes since the present climate of this coastal region is probably no more rigorous than that of southern Canada which has three species of the genus." However, such former northward distribution, while entirely probable, would have been possible only in a climate much milder than that which prevails at present. In Asia, *tunganus* on the mainland and *latiscutatus* on the island of Hokkaido extend north to about latitude 43°, and in North America, *fasciatus* extends slightly farther north. In order to have crossed between Alaska and Asia on presumed land bridges these skinks would have had to extend their ranges about 20 degrees north of their present limits, into what is now a cool climate. The winter climate of the Bering Sea is perhaps not much beyond the range of tolerance of the more cold-adapted forms of *Eumeces,* but the cold, cloudy, wet, and changeable summer climate is far beyond the range of tolerance of *Eumeces* or any other lizard.

It is highly improbable that the fossil record will yield direct evidence for the existence of a northern ancestral *Eumeces* of the *fasciatus* group. The characters by which the various forms are recognized are to be found mainly in details of pattern and scalation; the skeleton is so conservative that specific characters are ill defined or lacking even in well preserved fossil material. This hypothetical ancestor probably was a member of a deciduous forest community having components in common with the modern forests where the American and Asiatic species occur, along with types now extinct, and others which, though existing at the present time, have become separated from their original associates and occur in other regions.

Hollick (1936:11) has described a rich early Tertiary Alaskan flora strikingly different from that of the same region at the present time. Composed of genera now characteristic of warm-temperate to subtropical climates, it was remarkable in having many types of plants that are now most characteristic of the North American hardwood forests in the southeastern part of the continent. Besides such widespread genera as *Fagus, Betula, Ulmus, Platanus, Castanea, Corylus, Carpinus, Crataegus, Spiraea, Myrica, Smilax, Pinus, Picea,* and *Abies,* this flora included others now characteristic of both warm-temperate southeastern North America and Eastern Asia, as *Magnolia, Nyssa, Sassafras, Persea, Benzoin, Hamamelis, Liquidambar, Celastrus, Nelumbo,* and *Onoclea.* It included genera *Carya, Taxodium* and *Comptonia* that now are limited to SE North America, *Sequoia,* now limited to western North America, and also included several genera which at present are limited to southeastern Asia: *Ginkgo, Glyptostrobus, Cinnamomum, Hausmannia, Artocarpus, Dillenia* and *Koelreuteria.* This fossil flora provides strong evidence that in the early Tertiary climatic and habitat conditions as far north as Alaska were favorable for the existence of an ancestral *Eumeces* similar to the modern *E. fasciatus,* which might have given rise to both North American and Asiatic members of the *fasciatus* group.

There is abundant evidence for the existence of an Eocene land connection between Alaska and northeastern Siberia, permitting free interchange of faunas between the two continents, as shown by the almost simultaneous appearance of various mammalian groups in the fossil records of Asia and North America. Simpson (1947:627) has summarized the evidence that such intermigrations were occurring throughout most of the Tertiary, with occasional interruptions as in middle Eocene, and in middle and late Oligocene, and with increasing selectivity, chiefly a progressive tendency toward screening out of the groups less tolerant of cold (judged on the basis of their modern representatives). In the late Tertiary, and especially in the Pleistocene, animals known to have made migrations between North America and Asia were types now characteristic of boreal climates (*e. g.* pika, hare, vole, lemmings, marmot, jumping mouse, fox, wolverine, bear, moose, caribou, sheep, bison, camels, mammoth). Simpson believes that there was fairly strong climatic selectivity even in the Miocene interchanges, and he indicates several important groups that were non-migrants in the Miocene, most of them remaining so through the Pliocene and Pleistocene—the primates, Rhizomyidae, Gliridae, Viverridae, Hyaenidae, Dicerorhininae, Suidae, late Anthracotheriidae, Hippopotamidae, Tragulidae, Muntiacinae, Lagomerycidae, Giraffidae, and Bovidae. He states that there is good evidence that these are all mainly warm-climate animals which are not likely to have ranged in any force into a cold-temperate or boreal environment. In view of these conclusions it seems doubtful whether *Eumeces* or other reptiles could have crossed the Alaskan-Siberian land connection so late as the Miocene.

On the contrary, the climate and habitat conditions with which *Eumeces* might have been associated, although present as far north as Alaska in the Eocene, evidently had shifted far to the south by mid-Tertiary time. Axelrod (1950:230) has described a Miocene forest of the Columbia Plateau and northern Great Basin indicative of a uniform temperate climate and an average rainfall of thirty-five to sixty inches. This forest included: (*a*) various genera now characteristic of the southeastern hardwood forest or confined to it —*Carya, Castanea, Comptonia, Fagus, Liquidambar, Nyssa, Taxodium;* (*b*) other genera at present more characteristic of the western United States—*Sequoia, Lithocarpus, Pseudotsuga, Mahonia, Thuja, Gaultheria, Amelanchier;* (*c*) wide-ranging genera including *Alnus, Acer, Betula, Populus, Quercus, Picea, Pinus, Tsuga, Cornus, Ribes, Rosa, Hydrangea;* (*d*) modern east Asian genera, including *Ginkgo, Ailanthus, Glyptostrobus, Keteleria, Koelreuteria, Metasequoia, Pseudolarix, Pterocarya, Zelkova,* which were eliminated from the North American flora in the latter part of the Tertiary. In short, this western Miocene forest was remarkably similar in many respects both to the presumably ancestral early Tertiary Alaskan forest and the modern southeastern hardwood forest. The extent of this Miocene forest is unknown but judging from the sites where it has been recorded, it had progressed about halfway, both in latitude and in actual distance, from Alaska to the area occupied by the modern southeastern deciduous forests. Several other reptilian genera have distributions similar to that of the *fasciatus* group, with representatives in southeastern Asia and southeastern North America that probably have parallel histories of distributional divergence from early Tertiary northern ancestors similar to contemporary species (Schmidt, 1946:148-150). *Alligator, Natrix, Ancistrodon, Scincella, Elaphe, Opheodrys,* and within the genus *Eumeces,* the *obsoletus* group, all provide excellent examples.

EFFECT OF CLIMATIC FACTORS

Accounts of the habits and habitat, by various authors, indicate versatility in behavior, and adaptation to a variety of habitat conditions in different climates and plant associations. Some of the differences evidently result from the skink's tendency to maintain itself in surroundings of favorable temperature and humidity, which obviously are to be found in different types of situations at different extremes of the range. Hence even though the skink itself may remain unchanged, it tends to behave somewhat differently under diverse environmental conditions. Such environmentally enforced differences in habits would be difficult to distinguish from those having a genetic basis. Although no subspecies of *Eumeces fasciatus* have been recognized, local populations undoubtedly differ somewhat in size and other characters that have a genetic basis.

At the northern edge of its geographic range, *fasciatus* occurs in isolated colonies and seems to be restricted to open, rocky situations which receive the maximum amount of sunlight. Breckenridge (1944:96) wrote that at the two Minnesota localities representing the northwestern corner of the known range, the skinks were found at granite outcrops, and he mentions one found in western Wisconsin, at Taylor Falls, under an 18-inch slab of a basalt outcrop in sparse oak woods. Patch (1934:51) described a habitat at Arden, Ontario, among massive granite-gneiss domes, with sparse vegetation. At Point Pelee, Ontario, the species is common in the drier, more sparsely wooded situations, hiding beneath loose bark of stumps and logs.

Ruthven (1911:264) found *E. fasciatus* in the vicinity of sandy beaches in the Saginaw Bay region of Michigan. Elsewhere in its range it is more characteristically an inhabitant of hardwood forests, preferring the better drained and more rocky situations, according to the testimony of numerous authors. In eastern Illinois, Smith (1947:33) found it confined to the area south of the Shelbyville moraine, and not ranging into a prairie habitat. Near Elkville, Illinois, Cagle found the species abundant in higher and drier areas within sparse stands of oak in second growth woods, but it was absent from the low swampy areas adjacent to streams. Conant (1951:30, 210), describing the habitat in Ohio, stated that the species does not occur in swamps and areas that are subject to spring floods nor on dry hillsides, but is abundant in some areas where there are rotting stumps and logs remaining from former patches of swamp forest, and usually is found in low, moist situations, in wooded valleys or even at the edges of swamps and bogs. Lynn (1936:49) wrote that in Virginia, it is most often seen on steep, boulder-strewn hillsides and old sawdust piles. In the central Ozarks of Missouri, Owen (1949:49) found it abundant and saw it almost daily on rocky ledges, fallen timber, and fence rails, while *E. laticeps* was seen only once. Taylor (1936:59) wrote that *E. fasciatus* occurs where there is timber and is often found about fallen trees and rotting stumps, or about old sawmills where wood refuse has accumulated. Smith (1950:187) wrote that in Kansas the species is commonly found in wooded areas in moist situations about stones, leaves and rotten logs. Gloyd (1928:120) wrote that in Franklin County, Kansas, *E. fasciatus* occurred in upland situations and was the most abundant lizard where there were rocks, brush, or decaying wood. Gloyd (1932:401) also recorded it as abundant in the Pigeon Lake area, Miami County, Kansas, in wooded areas of sufficient elevation to be out of the river flood-plain.

HABITAT IN NORTHEASTERN KANSAS

In northeastern Kansas I have collected or observed this skink in several dozen localities, and searched unsuccessfully in numerous other localities. Absence of this skink, in some situations and its presence and relative abundance in others, provided a basis for appraising the environmental factors that are of critical importance. River valleys, of the Kaw and Wakarusa and their tributaries, with deep alluvial soil, alternate with flat or rolling upland some two hundred feet higher in elevation, and having shallow, rocky soil. Where the uplands slope to the valley floors, there are steep hillsides, usually with extensive limestone outcrops along their upper slopes. The alluvial plains formerly supported hardwood forests, while the hill slopes and uplands were largely prairie. At the present time the bottomland forest has been almost completely destroyed, as it grew on the most fertile and potentially productive soil, and has been replaced by cultivated crops. There are still trees along streambanks, and in occasional woodlots, but I have failed to find any skinks in such situations. I doubt that they ever have been numerous in the bottomland woods; lack of rocks for shelter, and periodic flooding are unfavorable factors. In the Kaw flood of June and July, 1951, for instance, the entire valley was inundated, and in smaller tributary valleys such as that of the Wakarusa, flooding is frequent at the season when skinks are incubating their eggs. The uplands, formerly prairie, now are used partly for cultivated crops and partly for pasture. The soil is poor and rocky, and now heavily eroded. The pastures mostly have a weedy type of vegetation indicative of overgrazing. Five-lined skinks are absent from most of this upland.

The steep slopes from the upland to the valley floor are now mostly wooded, and the population of skinks is chiefly in this band of woodland. Some of the hillsides that have relatively gentle slopes are treeless and are used for pasture, or are even under cultivation. Where second growth forest is present its aspect differs depending upon slope, exposure, and past treatment. Osage orange and honey locust are aggressive invaders on some dry hillside pastures, and in this type of woods the skinks are scarce or absent. Some hillside areas, especially on moist north slopes have thick second-growth woods, in which elm is usually the principal tree, with several oaks and hickories, walnut, hackberry, coffee tree, locust and osage orange, and with a dense understory vegetation of dogwood, gooseberry and coralberry, with vine tangles of grape, poison oak, and greenbrier. Such woodlands provide little food for livestock, and are often fenced off from adjacent pastures. The shading creates conditions unfavorable for skinks and they are relatively scarce in the denser woods. They are much more numerous in woodlands that are fenced in with pastures heavily grazed by cattle or horses, with understory vegetation kept cropped back, and with more open ground and patches of sunlight. However, they are absent or scarce in woods that have been subjected over periods of years to browsing, by sheep or goats, so heavily that hardly any herbaceous vegetation remains and so heavily that the soil is packed from trampling. Along the upper slopes, especially about heads of gullies, in areas strewn with flat rocks, in fairly open mixed woods, with some decaying wood on the ground, habitat conditions are most nearly optimum for the skinks. Artificial habitat features, such as rock piles, stone walls, wood piles, rail fences, or old deserted buildings and sheds, with loose boards lying about on the ground may support unusually high concentrations of skinks when the surrounding habitat is favorable.

STUDY AREAS

The University of Kansas Natural History Reservation where most of the field work for this study was done, has been described in a recent publication (Fitch 1952:8). While records were obtained from scattered points throughout the 590-acre Reservation and elsewhere in northeastern Kansas, field study of this skink was concentrated on four relatively small areas totalling only about ten acres in extent (Figure 26). These areas were selected on the basis of abundance and availability of the skinks, and of variety of habitat conditions represented.

One of these sites was a deserted quarry on a southward projecting spur of the plateau-like cuesta top, where the upper layers of the Oread limestone are prominently exposed. In the course of operations, begun about 1937, the area was denuded of trees and shrubs, and the upper layers of limestone were removed from a strip about 50 feet wide and more than 100 yards long. The exposed outcrop presented a vertical rock face five to ten feet high, with south and southeast exposure. Numerous jagged seams and fissures in the rock hastened its disintegration. Quarrying had been discontinued several years before the present study was begun in 1948. At that time there were talus-like accumulations of rock and soil several feet wide along the base of the rock face, supporting a luxuriant pioneer vegetation especially, sweet clover, stickleaf, ragweed and elm seedlings.

The habitat conditions provided by the exposed rock outcrop at the border of woods and open land, proved unusually favorable for reptiles in general, and it was one of the most productive sites on the Reservation for Sonoran skinks, collared lizards, racerunners, ring-necked snakes, blue-racers, bull snakes, pilot blacksnakes, scarlet king snakes, slender tantillas, copperheads, and timber rattlesnakes. For the five-lined skink, however, this disturbed area was marginal, and supported only a sparse population. Several decaying two-inch boards were preferred hiding places where the skinks were found most frequently, and remains of collapsed rock walls, one in the center of the area and one at the edge of the woods, were also occupied. Skinks may have tended to wander away to more favorable situations or may have been more subject to predation than those elsewhere, since the incidence of recaptures was relatively low. Most of the records from this general area were from a ledge in adjacent woods rather than from the quarry itself. Another site was a rock fill in a ravine below a pond made in 1937. This rock fill was 70 feet long, up to 30 feet wide, and three feet deep. East and north of the rock pile was a grassy dike, and beyond it the pond. On the west open grassland extended approximately 200 feet to the edge of the woods, with a diversion ditch at its border. On the south end, the rock pile was adjacent to woodland at the base of a steep slope with north exposure. On this slope the dense stand of second growth oak and hickory with an almost continuous leaf canopy was a poor habitat. The rock pile was thus partly isolated and surrounded by areas that were either uninhabitable to the skinks or supported only sparse populations of them. By 1948 the rock pile was partly covered by grape vines. Dead leaves and other debris had accumulated in the deeper interstices between the rocks. Spiders, beetles, snails and other small animals were extremely numerous in the vicinity of the rock pile and provided an abundant food supply. A large sycamore on the west side of the rocks provided some afternoon shade. This rock pile provided shelter for reptiles other than the five-lined skink—especially the garter snake, water snake, copperhead, and brown skink. Another area of about two and a fourth acres ("Skink Woods," Figure 21) was the one most productive of skinks. It is a wooded upper slope adjacent to a hilltop pasture. Along the hilltop rim the upper stratum of the Oread limestone presents a rock face as much as four feet high at the north end, but less exposed at the south end where it was partly covered by deposited soil. Approximately 100 feet down the slope a second outcropping is present, with many loose rocks and boulders throughout the whole area. Soil is light and loamy. The slope has a west exposure. The stand of trees is fairly open, with several large elms, walnuts, and yellow oaks, and occasional hackberries, ailanthus and red haws. This area was included in a narrow strip of woodland fenced about 1940 as a runway connecting a hilltop pasture with a valley pasture where water was available at a time when both pastures were heavily grazed by horses and cattle. As a result of trampling, browsing and grazing by livestock, understory vegetation of this area presented a different aspect from that in most other parts of the woodland. Saplings of the dominant tree species and shrubs, notably dogwood, gooseberry and crabapple, were relatively scarce. Herbaceous vegetation, especially muhly grass, was conspicuous. By 1953 in the fifth growing season after livestock were removed, the area still contrasted with other parts of the woodland in sparseness of shrubby vegetation. Old stock trails were still discernible, and some sheet erosion and gullying had occurred. The effect of livestock in holding back woody undergrowth seemed to be an important factor in improving the habitat as the skinks were much scarcer in adjacent woodlands on either side that were similar in species composition, size, and numbers of the larger trees, but different in having much thicker underbrush. These adjacent woodlands were not entirely comparable, however, because they had more north-facing exposures. Reptile associates in the Skink Woods area include the brown skink, Sonoran skink, glass-snake, worm snake, ring-necked snake, blue-racer, garter snake, pilot blacksnake, copperhead and timber rattlesnake, but only the worm snake and ring-necked snake were abundant.

Rat Woods, an area of approximately four acres, was like Skink Woods, formerly the upper part of a connecting strip between hilltop and valley pastures and was altered by the effect of concentrated trampling and browsing by livestock. It is V-shaped, with the apex at the north end, and the slope exposures southwest and southeast. The area is bisected from north to south by a small gully, and remains of an old rock wall. To the east of this gully the lower outcrop is prominent but west of the gully, it is but little developed. As compared with other wooded areas, this one was relatively dry. Trees, and other vegetation in general, are somewhat more xeric in aspect than are those in Skink Woods. Along the upper ledge are elms and hackberries, with many thick clumps of fragrant sumac. The trees are mainly elm, walnut, honey locust, and osage orange with hardly any oaks or hickories and, with shrubby undergrowth of dogwood, gooseberry, and coralberry sparser than in adjacent woodlands. Herbaceous vegetation consists largely of muhly grass, geum, and avens. On the hilltop edge above the ledge are many flat rocks of varying sizes, and the slope is thickly strewn with rocks, some of the larger ones deeply embedded in the soil. The population of five-lined skinks was relatively sparser than in Skink Woods. Other reptiles including the Sonoran skink, racerunner, glass-snake, worm snake, ring-necked snake, blue-racer, bull snake, pilot blacksnake, garter snake, scarlet king snake, slender tantilla, and copperhead, were more numerous in this area than in most other parts of the Reservation. The comparatively scarce prairie skink was found only in this area, and the scarlet king snake and slender tantilla were found only here and at the quarry.

The Annual Cycle of Reproduction and Growth

SEASONAL OCCURRENCE

Collectors and other observers have often noted that reptiles, in general, are not found in equal abundance throughout the entire season of their activity. Many kinds are most in evidence within a period of weeks after emergence from hibernation, which corresponds with the time of breeding and later they become much scarcer. In skinks of the genus *Eumeces* this tendency is perhaps even more pronounced than in most other kinds of reptiles. By midsummer or considerably earlier their period of greatest activity is passed, and in some kinds, adults, or individuals of any size can rarely be found in the latter half of the growing season, even by a skilled collector familiar with their habitats and habits. Thus, Taylor (1936:5) in the preface of his revision of *Eumeces*, describing the difficulties involved in assembling needed series of the many Mexican species by collecting on summer field trips, wrote: "In 1934 in western Mexico . . . I met with most dishearteninging results . . . (although more than 1500 specimens were collected) only a single specimen of *Eumeces* was taken. Hobart Smith, in 1934, accompanied by David Dunkle, made a journey into northwestern Mexico . . . and while generally successful, likewise obtained only a single specimen of *Eumeces*."

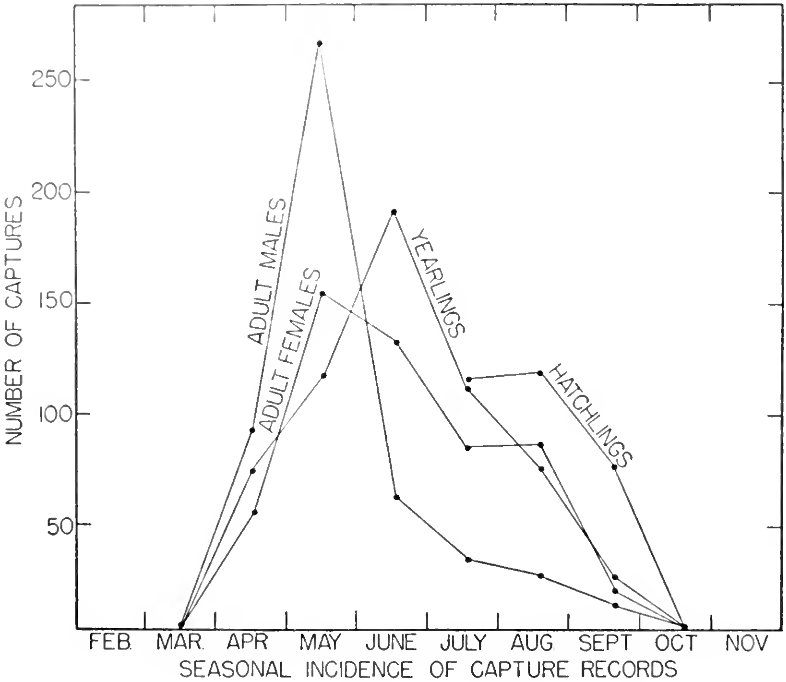

Fig. 7. Seasonal occurrence of five-lined skinks, based on data collected in 1949, 1950, 1951, and 1952; adult males and adult females are taken in greatest numbers in May, and in progressively smaller numbers through the summer and autumn; yearlings are found in increasing numbers through March, April, May, and June, then in decreasing numbers through the summer and autumn.

In the present study the tendency of *E. fasciatus* to concentrate its surface activity in early spring was clearly shown. In unseasonably warm weather in early spring, even in February in one instance, individual skinks have been found active on the surface or beneath flat rocks warmed by the sun; but general emergence ordinarily does not occur until sometime in April, depending on the weather. Unless the weather is much warmer than the seasonal norm, the skinks spend much of April in a torpid condition, either not becoming fully active until late in the month, or lapsing into torpidity with the return of cool weather after their first emergence from hibernation. During warm periods in April, however, activity is at or near its annual maximum for all individuals regardless of sex or age.

In May, with the advent of much warmer weather, daytime temperatures are usually high enough for the skinks to be active. Adult males travel about more actively and persistently than females or young, and as a result they are found so much more frequently that the numbers taken approximate those for adult females and young combined. Many of the adult males recorded in May were taken in funnel traps or pitfalls. Active males in the open were difficult to catch, and a high percentage of them escaped. To the casual collector or observer, these skinks are much more in evidence in May than at any other time of year, and most of those seen are adult males. By June, the numbers of skinks seen in the open decline abruptly. The adult males become relatively scarce, with reduction from more than half to about one-sixth of the total, and the young, about half-grown at that season, make up approximately half of the total. The adult females make up approximately one-third of the total June sample, but few of them were found active on the ground surface. Most were found in nest burrows beneath flat rocks. Under such conditions they tended to be sluggish in behavior, and were caught much more easily than were males and young. July was characterized by progressive decrease in the numbers of adult males, adult females, and second year young, whereby the numbers of each group were little more than half of those for June; and by appearance of a new crop of hatchlings which made up about one-third of the month's sample. Hatchlings first appeared from early July to late July in different years; few were recorded in July in some years. Females were much less commonly found in nests in July than in June because many nesting attempts were terminated before the beginning of July or early in the month, and probably because those that remained were often more deeply buried and better concealed. By August the adult males, and the second year young (by then approaching adult size) were found in still smaller numbers, but the number of hatchlings and of adult females approximated those recorded in July. In the females there is evidently some resumption of activity after the incubation period is terminated. The females are then hungry and sometimes emaciated, weighing less, on the average, than the year-old young of shorter snout-vent length. The numbers of hatchlings are augmented through early August in some years, as late broods continue to hatch. By early September few skinks except hatchlings are to be found, and activity continues to wane throughout the month.

In October skinks of any age or sex group are a rarity, even though temperature is about the optimum for their activity. Little is known concerning where and how they spend the fall months. Probably they are not actually dormant, but retreat underground where temperature is moderate and humidity is high. Individuals kept in captivity at this season were listless showing but little inclination to feed. The only five-lined skink taken on the Reservation in November was found in a funnel trap after a rain at the end of a long drought. It may have been attracted to the surface by moisture.

The following table shows the dates on which various events of the annual cycle were observed in each of five different years. Owing to the secretive habits of the skinks, these events generally were not observed until somewhat after their earliest occurrence in any one season. The lag was greater in some instances than in others.

Table 3. Phenology of the Annual Cycle in Five Different Years.

	1949	*1950*	*1951*	*1952*	*1953*
Earliest emergence from hibernation	Mar. 30	....	Mar. 24	Mar. 29	Mar. 20
General emergence from hibernation	....	Apr. 7	Apr. 14	Apr. 17	Mar. 27
Breeding coloration appearing in males	....	Apr. 15	Apr. 25	Apr. 28	Apr. 16
Peak of breeding season	May 3	May 12	May 16	May 10	May 7
Females starting nest burrows	May 26	May 24	May 19	May 19	May 24
Last appearance of gravid females	June 10	June 17	June 29	June 9	....
Earliest appearance of eggs	June 10	June 13	June 24	June 22	June 16
Earliest appearance of hatchlings	July 5	July 15	July 23	July 3	July 13
Latest hatching date	July 15	Aug. 8	Aug. 8	July 14	....
Latest fall record	Oct. 15	Sept. 19	Sept. 26	Nov. 9	Oct. 12

Sexual Cycles and Behavior

Reynolds (1943:370 and 1947:191) studied the histological and gross seasonal changes in the reproductive organs of the adult male *Eumeces fasciatus*. There is a well defined annual cycle. "Early seasonal increase in seminiferous epithelial heights and in diameter of lumina and tubules reached a maximum in April followed by regression reaching complete involution by August. Late seasonal revival of activity results, by November, in size of testicular elements comparable to those seen in January. Primary spermatocytes predominate in the germinal epithelium in January, secondary spermatocytes and spermatids in February, with spermatids and metamorphosing sperm dominating from March until late June when the germinal material of the current season is exhausted." Fifty-three adult males were used as a basis for his study. These were of diverse origins from Arkansas, Florida, Missouri, Tennessee, and Indiana. Since sexual cycles in such widely ranging species tend to be synchronized with local phenology, and change somewhat from one region to another, the seasonal cycle may have been somewhat obscured by the diverse origins of the material. The Florida specimens may have been of the species *E. inexpectatus*. Apparently Reynolds' experimental skinks were kept in captivity for varying lengths of time before their reproductive organs were examined. The normal cycle would almost certainly be altered in captivity, especially in skinks kept at high temperatures during the time that they would normally be hibernating.

The seasonal change in gross appearance of the testes is not great. In the breeding season the testes are slightly enlarged and are firm and engorged, with pinkish or orange tinge. In immature males, and adults that are not in breeding condition, the testes are smaller, attenuate, paler colored, and flaccid. Sizes of testes in some males killed in the breeding season are recorded in Table 4.

TABLE 4. SIZES OF TESTES IN SPRING AND EARLY SUMMER IN SEXUALLY MATURE AND JUVENAL MALES.

Date	Snout-vent length in mm.	Sizes of testes in mm.	Age class
May 6, 1951	76	7.0 x 4.0	old adult
May 20, 1951	77	5.0 x 2.8	old adult
May 20, 1951	74	6.2 x 3.2	old adult
May 20, 1951	74	5.5 x 3.0	old adult
May 20, 1951	66	5.0 x 2.8	young adult
May 20, 1951	65	4.2 x 3.2	young adult
May 20, 1951	64	5.3 x 3.1	young adult
May 20, 1951	45	2.5 x 1.0	juvenile
May 20, 1951	40	1.5 x .3	juvenile
June 3, 1951	65	5.0 x 2.5	young adult
June 10, 1951	67	4.0 x 1.8	young adult
June 25, 1951	75	4.0 x 2.0	old adult
June 25, 1951	70	3.5 x 1.8	young adult
June 25, 1951	51	2.0 x .5	juvenile

From the time of emergence in spring, males show some tendency to seek out females, and frequently a pair may be found together under the same rock, weeks before the onset of the breeding season. There is no satisfactory evidence that such associations have any permanence. At the time of emergence from hibernation the males rarely have even a trace of reddish coloration on their heads, and more than a month normally elapses before attainment of breeding coloration. Each year that observations were made activity of the skinks was interrupted by cold weather in April, so that the lizards were fully active for only part of the time between their earliest emergence and their attainment of breeding condition five to eight weeks later. The reddish suffusion of the breeding season, hardly showing in the first few weeks after emergence, appears suddenly within a few days in all adult males of the population. The best indication of the time necessary to attain breeding condition was provided by an adult male whose hibernation was interrupted on December 15 by bringing him into a warm room where he was kept at 80° F. or more in the daytime, and approximately 70° F. at night. Thirteen days later, on December 28, the male had developed a noticeable reddish suffusion. On January 3, nineteen days after hibernation terminated, the suffusion was near its maximum. When an adult female was placed with the male on this date, he showed sexual interest but the courtship was not consummated. On January 6, the 22nd day, the male's colors had reached their maximum, and when the female was placed with him, pursuit and copulation occurred promptly.

In the spring of 1952, the first skink of the season was found on March 29, still only partly activated, and under a large flat rock. Skinks were not caught or seen in any numbers until April 17, however, and general emergence probably occurred only a day or two earlier than this. On May 10, 1952, breeding activity was estimated to be at its peak. By May 28, the reddish suffusion was conspicuously faded in several males taken. By June 10 it was no longer discernible.

In the immature female the oviducts are small and threadlike, and the ovaries have grapelike clusters of pale whitish eggs, which are minute, often less than .5 mm. in diameter (Figure 8A). In sexually mature females ova enlarge rapidly after emergence from hibernation in the spring. While eggs are still in the ovary, they are approximately spherical. In late April and early May the developing ova enlarge rapidly. Approximate average sizes (dimensions in mm.) of developing ovarian ova in each of 22 mature females on different dates were as follows: April 17, 1949: 2.6, 2.3, 2.2, 2.2, 1.9, 1.9; April 18, 1949: 2.2, 1.9, 1.8, 1.1, 1.1; April 24, 1949: 4.6, 3.2, 2.5, 2.3; May 6, 1951: 2.5, 2.3; May 20, 1951: 7.0, 6.2; May 25, 1951: 8.0; June 3, 1951: 6.0, 5.5.

The two females containing ovarian eggs on June 3, 1951, were retarded individuals, taken along with several others that had already ovulated. Copulation takes place in early May before the ova have grown to their full size. In the following weeks both the ova and the oviducts enlarge rapidly. Upon passing into the oviducts, the ova assume an oval shape and are approximately 9 by 6 mm. before the albumen and shell are added. Deposition of a clutch of eggs probably extends over only a day or two at most, as clutches appear abruptly in the nest cavities. On only a few occasions were the females found in nest cavities with their clutches partly laid.

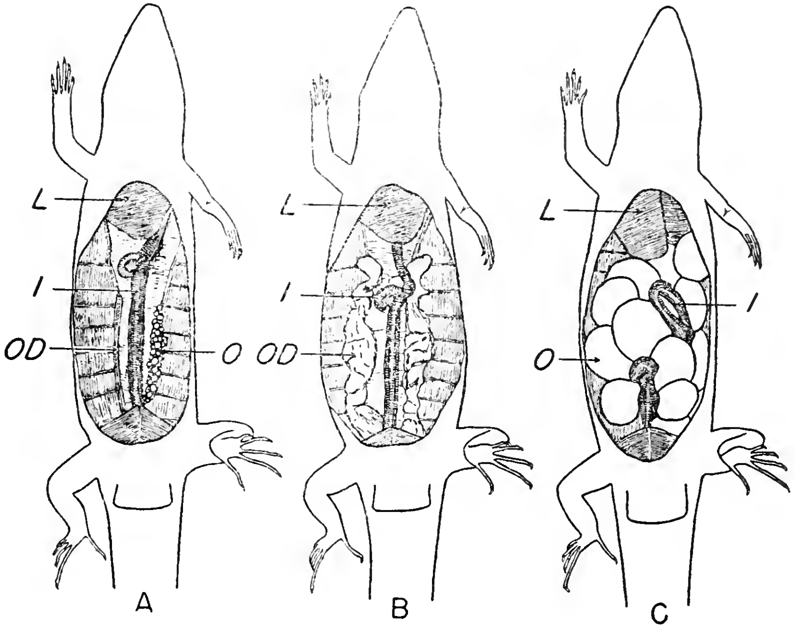

FIG. 8. Adult female skinks with ventral body walls removed to show reproductive organs. A. Condition in April shortly before the breeding season; the ovary (O) is still small and elongate, with the small ova forming a grapelike cluster; right ovary removed to expose the small bandlike oviduct (OD) beneath it. B. Condition in late May shortly before ovulation; the greatly enlarged ovaries are removed to expose the oviducts (OD) now enlarged and convoluted for reception of the ova. C. Same stage as B, with mature ova (O) filling most of the body cavity and concealing other internal organs, I—intestine; L—liver; approximately natural size.

Sexual behavior is for the most part limited to a short period of weeks in spring. In an average year in the area of the study the first two weeks of May would include the peak and the greater part of the breeding season. The "courtship," such as it is, and mating have been described by many observers. However none of the published accounts seems to include all the essential features in their usual sequence as observed in the present study. It has been brought out by the studies of Noble and Bradley (1933: 94), Noble and Teale (1930: 54) and Schmidt (1933: 71-76) that the sexual behavior of lizards has phylogenetic significance. Certain basic patterns in mating behavior are characteristic of saurian families, other traits are characteristic of genera, while certain details may be characteristic of species, or perhaps even of subspecies.

In the breeding season the adult male directs the greater part of his activities to a search for females, and finds them by both sight and scent. Observations on searching males suggest that they trail females by scent to some extent, or at least detect their presence in the general vicinity by this means. Upon discovering a female, the male pursues her with vigor and determination unless the temperature is too low, or unless he is not at the height of breeding condition. The female makes no positive response but reacts to the male's presence by fleeing, either frantically or perfunctorily, but if she is physiologically ready to breed the reaction is usually somewhat intermediate between these extremes. The first reaction of the male as he approaches the female is to touch her with his tongue, apparently receiving olfactory stimuli which are essential to the mating pattern. Rushing in pursuit of the female he then attempts to seize her in his jaws. Most often a preliminary grasp is secured on the female's tail. The female may resist vigorously, wriggling and clawing, turning upon the male to bite or to threaten with her gaping jaws. At the first opportunity the male deftly shifts his grip from the female's tail or hindquarters to a more anterior position, which may be as far forward as the forelimbs or may be as much as an inch behind them, a little to one side of the mid-dorsal line. The male secures his hold by pinching loose skin into a small fold. Having gained this position the male is more or less out of reach of the female's jaws, and after a brief struggle both rest quietly except for their rapid breathing, usually for a minute or more, the ventral surface of the male resting on the female's dorsal surface. The male suddenly thrusts his tail beneath that of the female. His hind leg then rests over the base of her tail and the right angle formed by the laterally projecting hind leg and the tail in each lizard aids to guide their hindquarters into position so that cloacal contact is established. Copulation then begins immediately. The male's body may be bent in a semicircle, to one

PLATE 1

Fig. 1. Habitat of *Eumeces fasciatus* near the center of the "Skink Woods" study area on the University of Kansas Natural History Reservation, a glade with loose rocks that were used as nesting sites and shelter by many five-lined skinks.

Fig. 2. A log on rocky slope in open woods with sparse undergrowth, fifty feet from center of glade shown in Fig. 1. The trees are mostly oaks (*Quercus Muehlenbergii*). The decaying log in middle foreground is much frequented by the skinks as a shelter and source of insect food.

PLATE 2

FIG. 1. Old adult male, year-old young and hatchling in July, showing differences in size and pattern.

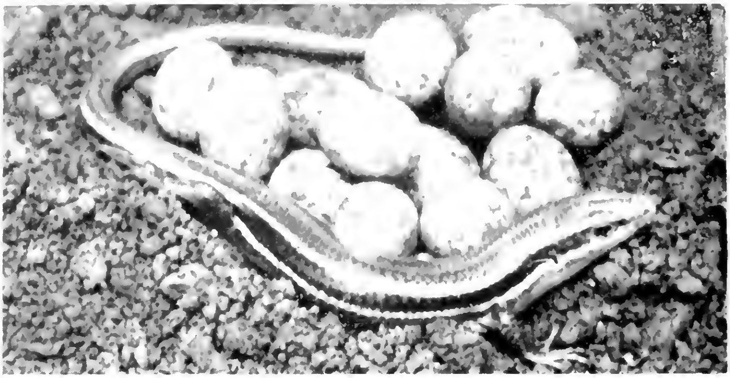

FIG. 2. Adult female skink in a natural nest, with her clutch of eggs late in incubation. The nest cavity is excavated in loose soil beneath a flat rock, which was raised momentarily to expose the nest to view.

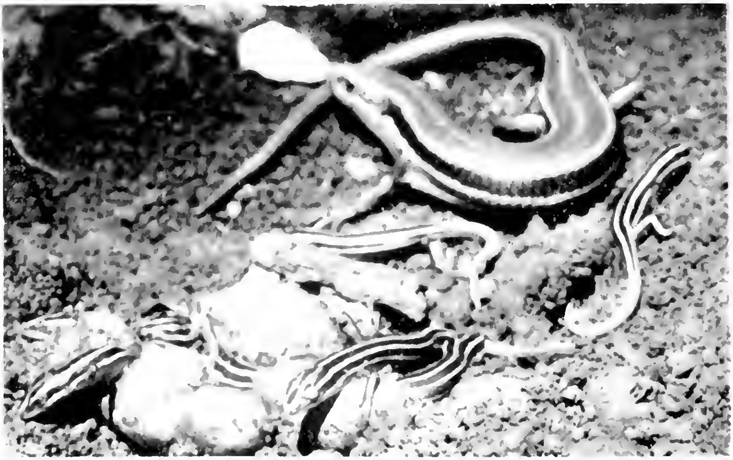

FIG. 3. The same female and nest, with eggs in process of hatching.

side of the female, or may be in an S-shaped loop, depending on whether or not the hemipenis employed is on the side opposite to that on which the female is grasped. Only one hemipenis is inserted, but occasionally the other may be everted also. As copulation begins the male's hind leg, flexed over the female's tail base quivers, but otherwise there is hardly any movement during approximately the first one-third of the copulatory period, and this phase may last for from one to three minutes. Then, abruptly, the male begins rhythmic, jerky flexions of the proximal portion of the tail, at the rate of approximately one per second. These tail movements are in a dorsoventral plane, and there is no perceptible movement of the body. Shortly after these movements cease, contact is broken usually at the initiative of the female, as she suddenly struggles to escape and is released either immediately or after a few seconds by the male. She then moves away, pressing her cloacal region against the ground. Her movements have become unhurried, with little or no attempt to avoid the male's attention. The male usually follows, either close behind, or straddling the female's tail or body. He may nip at her tail or body repeatedly, but without securing a grip. When the female pauses, he may come to rest with his chin or forequarters resting on her. Usually the association does not last more than a few minutes.

Noble and Bradley (1933: 77) mention frequent homosexual matings between captive males. However, I observed no homosexual matings, either under natural conditions or in confinement. The pugnacious behavior of males that are in breeding condition ordinarily would prevent homosexual mating. Males in such weakened condition as to be unable to defend themselves effectively might evoke sexual attack, instead of the usual fighting response in other males. Although no actual experiments were performed in the present study in connection with the courtship and mating behavior, accounts of some workers seem misleading. My own observations indicate that the capacity for sex discrimination in this particular kind of lizard, and probably in others, has been underrated. For example, it has been stated that the male rushes with open mouth at the neck of any other skink that happens to be around, and he identifies it as a male if it fights back, or as a female if it does not. On the contrary my observations indicate that sex recognition occurs almost as soon as the male is aware of another skink's presence. The red head of the breeding male is an excellent example of a social releaser in the sense that this term was used by Tinbergen (1948: 8). Like the red belly of the breeding male stickleback, it facilitates sex recognition and evokes hostile behavior on the part of other males. Courtship, mating, and fighting reactions however, seem to be evoked by the interaction of a complex of social releasers. Whereas males and females are strikingly different in appearance in the breeding season, visual sex recognition is complicated by ontogenetic changes. The body stripes characteristic of the female pattern, become dull or even disappear in some old females, which then approximate the typical male pattern. On the other hand newly matured males in their first breeding season retain distinct body stripes of the female pattern. Their sex is evidenced mainly by their reddish facial suffusion, which is not quite so extensively developed as it is in older individuals. Also, in these newly matured males the temporal region is not so swollen as it is in old males.

The male whose dormancy was terminated in early winter by bringing him into a warm room causing him to assume breeding coloration and to breed some four months earlier than those under natural conditions has already been mentioned. By the time the regular breeding season arrived, this male had long since undergone sexual regression and retained no trace of the red suffusion. In this condition, placed in a terrarium with a mixed group of breeding adults, his social status was of unusual interest. He exhibited no interest in the females and was less pugnacious toward other males than were the individuals in breeding condition. Although he seemed somewhat more nervous and timid, his hostile behavior was not entirely suppressed, as from time to time he moved up to other males and bit them viciously. His color pattern resembled those of certain old adult females in which the body stripes have been suppressed, but the breeding males evidenced no uncertainty as to his sex and were uniformly hostile. Their reactions were not noticeably different toward him than they were toward breeding males. The importance of an olfactory stimulus as a social releaser in sexual behavior of lizards has not been appreciated, although Noble and Mason (1933: 10) did demonstrate its importance in the behavior of the female toward her eggs.

It is evident from published accounts, and from my own limited experience with *fasciatus* in parts of its range other than northeastern Kansas, that the phenology of the breeding cycle is subject to geographic variation, synchronizing with the somewhat different climatic conditions under which the species occurs. However, the difference is less than might be expected, in view of the species' extensive range. As a result of the early spring, and the warm summer climate in the southern states, dates of laying and hatching may be several weeks advanced. On April 12, 1952, Dr. Wilfred T. Neill showed me several live *E. fasciatus,* collected a few days before along the Trinity River in southeastern Texas, which appeared to be at the height of breeding condition. In northeastern Kansas on that date, general emergence had not yet occurred, and it was not until about May 10 that the population attained the peak of breeding condition. On May 8, 1948, near Burr Ferry, Vernon Parish, Louisiana, I caught an adult female in her nest burrow, and she contained eggs ready to be laid. Data with which Mr. Robert Gordon kindly provided me for specimens from southern Louisiana and southeastern Texas, in the Tulane University collection, indicate gravid females on June 4, 1952, and June 17, 1948 (3), and females with their egg clutches on June 16, 1948, June 17, 1948, June 23, 1950; and hatching dates in captivity of July 19, 1949, July 19, 1950, July 25-26, 1949. These dates correspond well with those for specimens obtained in northeastern Kansas in the same years. In the northern part of the range, Ruthven (1911: 264) recorded that in the Saginaw Bay region, females taken on June 19 had eggs nearly ready to be laid, and after July 2 clutches were found frequently; young of the year were first observed on July 31. A juvenal specimen in the University of Minnesota Natural History Museum, collected on August 11, 1938, at Dresser Junction, Wisconsin, is 30½ mm. in snout-vent length—approximately the size of juveniles in northeastern Kansas at the same season. Evans and Roecker (1951: 6) record hatching as occurring in the first week of September at Arden, Ontario, indicating that at the northern edge of the range hatching may be delayed as much as two months. With such delayed hatching, but little time remains for the young to grow before they are forced into retirement for hibernation.

FIGHTING

Territoriality in the usual sense is lacking in the five-lined skink, and could scarcely exist in an animal of its habits. To defend a definite area (territory) against intruders of its own species, the animal would have to detect such intruders promptly. The skink, however, is so secretive in habits that at any given time the individual is likely to be hiding and inactive, even when conditions are favorable for it to be in the open, and other individuals therefore can then wander onto its home range unopposed. Even when an individual is active, it lacks the ability to detect others, except within a radius which would encompass only a small fraction of the entire home range. The senses are inadequate to inform one lizard of the presence of another until the two are only a few yards, or even a few inches apart. Usually the lizard is on the ground, where even small objects obstruct its view, and vision is probably effective for only a few yards. Hearing is probably effective for about the same radius in detecting animals of approximately its own size. Scent is effective in detecting prey near at hand or on contact, but probably does not serve for detection of other lizards that are not in the immediate vicinity. Therefore, the area covered by one in the course of its normal activities may harbor many others, and individuals most of the time are unaware of the others on their home ranges.

Under most circumstances these skinks behave toward each other with tolerance or indifference, but during the breeding season adult males become hostile, and fight on sight. Their reddish facial suffusion serves as a social releaser which elicits hostile behavior and facilitates sex recognition. As the breeding season wanes, the reddish suffusion fades rapidly and male hostility, probably controlled by the same hormonal complex, is likewise suppressed. Hostile behavior is rare in adult females or young at any time.

Combats and pursuits have been observed most frequently the last week of April and especially in the first two weeks of May. At this season funnel traps set along rock ledges often caught two adult male skinks together. In almost every instance one of the two confined males was mutilated, with pieces of skin and flesh bitten from the tail and with chin, snout, and neck scarred; most serious wounds were usually in the sacral region or base of the tail or both. Often the wounds were so severe that the skink died in a short time in captivity and presumably others that were released died also.

On April 28, 1949, a large adult male skink, chased by another, ran out in the middle of a trail and stopped. The pursuer stopped a few inches from it, then after a long pause, retreated in the direction from which it had come. For the five minutes that the pursued skink was watched, it lay motionless, partly hidden by dry leaves, evidently seeking to avoid further pursuit by concealment. I caught it without difficulty, and it seemed weak and dazed, as if injured in the fight. Its reddish suffusion was conspicuous, but not fully developed.

On May 3, 1949, an adult male having bright red facial suffusion was observed searching persistently in ground litter; he was seen to find and pursue a female, and to copulate. A few minutes after mating was completed and the pair separated, a second male also searching in the vicinity came within sight of the first one. The two noticed each other at a distance of about 18 inches, indicating their awareness by their more alert, jerky movements, and spasmodic vibrating of their tails. The newcomer darted at the other, and for a moment they dodged and sparred. As one broke away to run, the other seized it by the tail. They were on an exposed tree root about an inch in diameter. The skink that was caught twisted its body around underneath the root and seized its adversary by the tail likewise, so that their linked bodies encircled the root, each squirming to disengage itself from the other's jaws. After a few seconds they did break apart, and then maneuvered briefly menacing each other at close quarters, but they gradually moved away and lost contact.

On May 10, 1949, two adult males were seen to approach each other slowly, pausing for perhaps a minute when they were a little more than one foot apart. Then one edged up to the other, and with a sudden lunge seized it by the head. The one seized broke away with a vigorous jerk, and promptly retaliated by biting the first one's head. After a few seconds of rapid sparring and thrashing, they broke apart, and one chased the other for several feet until it eluded further pursuit by dodging and hiding.

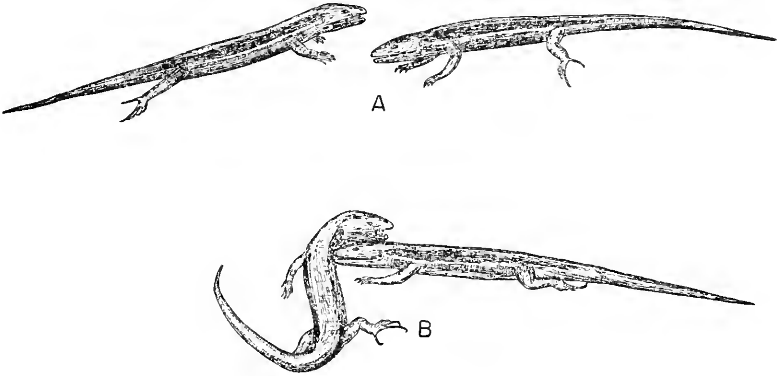

FIG. 9. Adult male skinks fighting. A. Menacing approach. B. One has lunged and secured a grip on the other's side, holding it at right angle. The one caught is unable to flex its body and neck enough to secure a retaliatory grip on the attacker, and must break away by violent thrashing.

On May 12, 1950, my attention was attracted by a rustling in dry leaves. Within a few inches of my foot two adult males were struggling fiercely with jaws interlocked. Sudden violent twisting and thrashing alternated with quiet periods of a few seconds duration, in which the lizards scarely moved except for heavy panting and twitching of their tails. After perhaps two minutes of fighting, one broke away and ran. For a distance of several feet it was closely pursued by the other, which, however, soon lost contact with it in the rough terrain and surface litter.

On May 12, 1951, rustling in dry leaves attracted my attention to two large adult males fighting. For about fifteen minutes that they were observed, they struggled, with neither yielding ground, though they thrashed and rolled about over an area of several square feet. Sometimes they were disengaged for short intervals. Then facing in opposite directions, with their heads side by side, they would snap at each other's necks and shoulders (Figure 9). Part of the time both males had grips and were biting each other simultaneously, but more frequently one or the other had a temporary advantage. When one secured a grip it would strain to the utmost, biting as hard as it could and lunging forward with frequent short jerks, meanwhile striving to keep out of reach of the other's jaws. The one caught in the attacker's grip was usually unable to flex its body sharply enough to reach its opponent at all, or could barely reach it at such an oblique angle that its jaws slipped off the smooth body. Sometimes the one held did succeed in catching the other's front foot. The one caught in the other's jaws always succeeded in tearing loose after a short time. In the interval while the attacker rested with jaws partly relaxed, the victim had an opportunity to break away. Even when both were free, they did not obtain grips easily, but often made several unsuccessful lunges and bites, the jaws of each slipping off the firm, smooth sides of its opponent. Sometimes the attacker seized a fold of skin, or sometimes obtained a wide grip on its body. One which had obtained a grip sometimes rolled rapidly, spinning the other around and dashing it against the ground. As these rotations stopped, the victim might come to rest on its back in such a position that it was temporarily helpless, but always broke loose after further struggles. Neither showed any inclination to retreat until finally, when they were interlocked, rolling about almost at my feet, I attempted to catch them. Then they instantly disengaged and rushed away, and one escaped. The one caught had suffered but little injury in the fight. Numerous tooth marks were discernible as minute abrasions on the surface of the scales, but the bony dermal armor had not been perceptibly penetrated during the prolonged and violent struggle.

EGGS

The eggs of *Eumeces fasciatus* are like diminutive chicken eggs in appearance. They are white when first laid, slightly translucent when held to the light. Within a day or two after they are laid, these eggs are soiled to a dull tan color, somewhat mottled, as a result of being rolled and dragged about in contact with the floor and wall of the nest burrow. Like the eggs of most other reptiles, those of *Eumeces fasciatus* have parchmentlike shells. These shells are thin and easily punctured. As incubation proceeds, the egg enlarges by gradual absorption of moisture and the somewhat elastic shell is stretched. An egg left in water for as much as a day does not gain in weight appreciably. Except for occasional abnormal ones, the eggs of any one clutch are notably uniform in size and shape at the time they are laid. As incubation proceeds, some eggs enlarge more rapidly than others, and attain larger ultimate size. Differences in shape also appear, some eggs becoming relatively elongate and thin, while others are thick and blunt. Some become distorted to asymmetrical shapes. In nests that have been deserted by the females, eggs of irregular shape are especially noticeable. It seems probable that the frequent shifting of the eggs by the female prevents unequal drying or stretching in different areas of the shell. Normal young were observed to hatch from grossly misshapen eggs. Under conditions of drought, the eggs may not enlarge normally during the latter part of incubation, and may become indented or partly collapsed, and yet apparently normal young hatch from them. Both in the field, and in laboratory experiments, eggs were found to have remarkable tolerance for excess moisture. After heavy rains of summer thunderstorms, nests were sometimes found to have water trickling through them, and on occasion eggs were found to be partly submerged in water in the nest cavity. Exposed rocks at the heads of small gullies often were chosen by the female skinks as the shelter for their nests. In these situations the nests were exposed to run-off water. In July, 1951, especially, unusually heavy precipitation resulted in the flooding of many nests. In some instances desertion by the females and destruction of the eggs seemed to have been caused by this flooding, even in the well-drained hillside situations where this study was made.

The extent of tolerance to immersion in water probably depends on the stage of development, the temperature, the oxygen content of the water and other factors. One egg was fully immersed for ten minutes on July 20, 1951, then returned to a container with damp soil in the laboratory, where it seemed to develop normally. On July 30 it was opened and found to have a living fetus,

TABLE 5.—MEASUREMENTS IN MILLIMETERS AND WEIGHTS IN GRAMS OF EGGS IN THE SAME CLUTCH AT DIFFERENT STAGES DURING THEIR INCUBATION, SHOWING GRADUAL INCREASE IN SIZE.

	June 17 (laid)	June 18	June 24	June 28	July 17	July 20	July 28	July 30 (hatched)
Average length (for 7)	......	....	......	......	13.7	14.3	14.7	......
Average width (for 7)	......	....	......	......	10.5	10.9	11.1	......
Typical length	......	11.1	......	12.5	14.0	14.3	14.8	......
Typical width	......	7.5	......	9.9	11.0	11.2	11.0	......
Maximum length	......	11.5	......	......	14.5	15.0	15.5	......
Maximum width	......	7.5	......	......	10.9	11.1	11.4	......
Minimum length	......	10.5	......	......	12.5	12.8	13.5	......
Minimum width	......	7.0	......	......	9.9	10.0	10.5	......
Average weight	......	$.38^{10}$	$.58^{5}$	$.63^{9}$	$.82^{8}$	$.90^{7}$	1.0^{7}	......
Typical weight	......	.4	......	......	....	.9	1.0	......
Maximum weight	......	....	......	......	....	1.0	1.1	......
Minimum weight	......	....	......	......	....	.7	.7	......

Superior number indicates the number of individuals averaged.

which was a week short of hatching. On July 22 another egg of the same clutch was immersed and left in water for 23 hours. On July 30 it was ruptured in handling and found to contain a living fetus. On July 31 two eggs were placed in a dish of water in a refrigerator. On August 5 they were removed and opened. Fetuses were dead and were not appreciably larger than the one of the same clutch in the egg opened on July 31. On August 5 two of the remaining eggs of this clutch were placed in a Petri dish, partly immersed in water, with approximately one-fourth of the surface of each protruding and exposed to the air. Forty-eight hours later it was found that both eggs had hatched. Evaporation had reduced the water in the dish to an amount sufficient to cover only about the lower one-third of each egg. One hatchling was missing, evidently having climbed out of the shallow dish and escaped to the floor. The other was found still standing in the water with its head protruding, and it was lively and in good condition. The remaining four eggs in this clutch, which had been kept in a container of damp earth, were also hatching on this date. On July 10, 1952, an egg in a late stage of incubation was immersed in water in the laboratory. On July 14 when removed, it had fungus growing on it, and was found to have a dead fetus, nearly full-sized.

The range of temperature tolerance of the embryo is wide, probably comparable to that of the adult. Time required for incubation is dependent on temperature. Persistently wet and cloudy weather in the summer of 1951, keeping temperatures relatively low in nests, was a contributing cause to late hatching that summer. As compared with 1952, hatching was about one month delayed in 1951, but later emergence and breeding accounts for part of the difference. The extent to which low temperature may delay incubation was indicated by the effect of refrigeration on several experimental eggs, as recorded below.

1.	July 8, 1952	Egg transferred from natural nest to jar of damp soil in refrigerator at 13.8°C.
	July 14, 1952	Seems to be in good condition.
	July 19, 1952	Partly collapsed. Weight and measurements same as on July 8; opened and found to contain a dead fetus. Snout-vent length 23 mm., forehead bulging, skin delicate and membranous. Colors somewhat dull, indicating that it was not quite fully developed, although it had attained the minimum hatching size.
2.	July 10, 1952	Egg from natural nest (15.0 x 10.5 mm., .95 gm.) put in refrigerator at 11.6°C. Control (14.5 x 10.6 mm., .8 gm.) from the same clutch kept in hatching medium in laboratory.
	July 13, 1952	Control egg hatching; refrigerated egg shows no indication of hatching.
	July 14, 1952	Experimental egg 15.8 x 10.8 mm., 1.0 gm., seems to be in good condition. Nest from which it was taken found to have all remaining eggs hatching today.

	July 19, 1952	Experimental egg 15.0 x 10.0 mm., 1.0 gm., removed from refrigerator and transferred to container in damp rotten wood in laboratory. Seems to be in good condition.
	July 23, 1952	Experimental egg found to be hatched this morning, and hatching must have occurred either in the night or late yesterday. Eggshell still damp and pliable.
3.	July 10, 1952	Egg from natural nest (14.0 x 10.5 mm., .8 gm.) put in refrigerator at 11.2°C., in container with damp decayed wood. Control egg (14.2 x 10.1 mm., .8 gm.) from the same clutch kept in the same hatching medium in the laboratory.
	July 12, 1952	Nest from which experimental and control eggs were taken has started to hatch, and two hatchlings were seen there.
	July 13, 1952	Control egg hatched.
	July 14, 1952	Experimental egg 14.2 x 10.1 mm., .8 gm., seems to be in good condition. Nest in field examined and all eggs were hatched, with only three of the hatchlings remaining, the others having dispersed.
	July 19, 1952	Experimental egg 14.0 x 10.0 mm., .95 gm., still appears to be in good condition; removed from refrigerator and kept in laboratory.
	July 23, 1952	Experimental egg found to be hatched, and hatchling active although still in hiding beneath rotten wood. Probably it hatched early in the day of July 22; the empty shell is still moist.

These experiments seem to show that, in the later stages of incubation at least, lowering of temperature to 11° or 12° C. almost halts development of the fetus. Harm does not necessarily result, however, and when again warmed to normal incubation temperatures, the eggs eventually hatch, the incubation period being lengthened by a time approximately equivalent to the interval of refrigeration.

Under natural conditions the time required for incubation probably varies within wide limits, controlled mainly by temperature. No two clutches receive the same amount of heat, as sites differ greatly in extent of insulation, and exposure to sunlight. Each year, earliest appearance of hatchlings is in a warm, sunny situation, and in cooler, well shaded places hatchlings appear somewhat later. Their incubation is evidently somewhat protracted, although later emergence from hibernation and later breeding of adults in these situations might also contribute to the delay.

Widely different incubation periods have been recorded in the literature and the variation probably is not due to temperature alone. Noble and Mason (1933:4) recorded incubation periods for six females from the same locality, and evidently kept under the same laboratory conditions, as 47, 41, 36, 29, 29, and 27 days. Despite the wide difference in incubation time, all six clutches hatched within a 12-day period from July 5-17. It seems improbable that differences in temperature account for the 20-day disparity between maximum and minimum incubation time, in these females kept under similar conditions. Cagle (1940: 229) recorded an even shorter incubation period for one kept in the laboratory, which laid eggs on June 30; hatching occurred on July 23 and 24. Retention of eggs in the oviduct by females kept under unnatural conditions would partly explain their late laying and the short incubation period of their clutches. Such ability to retain eggs in the oviduct while their development proceeds would not be especially surprising in *E. fasciatus* since its congener *E. lynxe* of the highlands in southern Mexico is normally ovoviviparous (Hartweg, 1931:61; Taylor, 1936:171). Cagle did not determine incubation time for any of the natural nests found, but evidently in all of them laying occurred earlier than in the single female brought to the laboratory while still gravid. All the eggs in natural nests found by him were brought to the laboratory and most of them were hatched. Cagle remarked: "The fact that these 26 nests hatched within a period of nine days seemingly indicates that the egg laying period extends over not more than two weeks."

In the present study no incubation periods so short as those recorded by Noble and Mason, and Cagle, were observed. Incubation times were recorded for clutches both in the laboratory and in the field, but for most of the clutches only approximate incubation periods were recorded. Failure to record the exact date of laying or of hatching, or both resulted from attempts to avoid frequent disturbance of females in their nests, which might have caused them to desert.

One clutch of eggs laid in a terrarium probably on June 17, 1951—possibly a day or two earlier—hatched on July 30, after an incubation of about 44 days. Another clutch, found in a terrarium on July 17, 1951, was estimated to have been laid about a week earlier, judging from the average length (11.8 mm.) and average weight (.55 gm.) of the eggs. These eggs hatched on August 9, a little more than three weeks after their discovery. A clutch found in the field on June 25, 1951, evidently recently laid (average length 12 mm., weight .45 gm.), hatched 41 days later, on August 5. Another clutch found in a terrarium on July 17, 1951, was estimated to have been laid ten days or two weeks before, as the average length was 12.7 mm. The eggs hatched on August 7, three weeks after their discovery. On June 25, 1951, an incomplete clutch of three eggs was found with a female which still had an unlaid egg. The three eggs probably had been laid the same day or the day before. They were kept in the laboratory and weighed and measured at intervals until July 28, 33 days after their discovery when both those that remained were accidentally punctured and found to have nearly full term fetuses. In the field a nest which contained only a gravid female on June 24, 1951, had a clutch of eggs already mud stained and slightly enlarged on June 29. The most probable date of laying was June 26. On August 6 the eggs had all hatched but several young were still in the nest. Probably most hatched on August 5. The incubation time was hence approximately 40 days.

On June 21, 1951, a natural nest was found with eggs already somewhat enlarged (12.5 x 8 mm.) and mud stained. This nest was checked from time to time in the next few weeks, and after 39 days, on July 30, it was found that all the eggs had recently hatched, but six young were still in the nest cavity.

Another nest was found on June 24, 1951, with the eggs already markedly enlarged (14 x 8 mm.) indicating that laying must have been several days earlier—probably well over a week. Hatching occurred approximately 34 days later, probably on July 28, since on July 26 there was no sign that hatching was imminent, and on July 30 only the empty dried eggshells remained in the nest.

The incubation time approximated six weeks for those nests with most complete records. Under wet and stormy weather conditions such as prevailed in 1951, this may have been the normal incubation period, but in warmer and drier years incubation time is shortened.

In the five-lined skink each adult female normally produces one clutch of eggs annually. The size of the clutch produced is subject to individual variation, and is influenced by the age, size and condition of the female. Geographic variation in clutch size might also be expected. Data were obtained from breeding females killed and dissected, from counts of eggs found in natural nests in the field, and from clutches of eggs laid by females kept in captivity. For the total of 115 recorded clutches represented by the combined data from all these sources, the average number of eggs per clutch was 9.5.

In many females dissected for the purpose of obtaining egg counts, ovulation had not yet occurred. The ovarian eggs present in each of these females included two main size groups, the larger ones in process of maturing and evidently destined for deposition in the current season, and minute, immature ones. A few of intermediate size were always present, however, resulting in uncertainty as to the size of the clutch being produced, especially when development had not proceeded far. Even when the larger eggs formed a fairly distinct size group, some usually were well below maximum size. Relatively high counts of clutches were obtained from these examinations of enlarged ovarian eggs. Evidently development frequently is arrested, and resorption may occur before ovulation. As a result the numbers of ovarian eggs developing are a poor indication of actual clutch size. A series of gravid females were obtained and examined after ovulation; the numbers of eggs in their oviducts probably indicates accurately the sizes of their clutches. Gravid females taken from their nest burrows and kept in the laboratory in containers with loose damp soil soon excavated new burrows and deposited clutches. Many natural nests were found in the field, and the egg counts obtained from them provided further data concerning clutch size. Although most of these clutches probably had their full complements of eggs, others certainly had sustained losses to predators, or to the females themselves, which may eat some of the eggs. Therefore the average number found is erroneously low. Some of the natural nests found may have contained two or more clutches or parts of them, and the higher counts obtained from natural nests therefore are also questionable.

For different sets of data on clutch size, numbers were as follows:

TABLE 6. SIZE OF CLUTCH.

SOURCE OF SAMPLE	Number of clutches	Mean	Standard deviation	Maximum	Minimum
Early ovarian....	25	11.4 ± .46	2.28	20	5
Late ovarian, uterine, or laid in captivity....	56	9.16 ± .21	1.85	15	4
In natural nests..	34	8.82 ± .32	1.85	16	4

On the average, larger females produce more eggs per clutch than do smaller females. Of 49 females for which measurements were recorded, and which had uterine or large ovarian eggs, 31 were 70 mm. or more in snout-vent length. These 31, mostly or entirely old adults, averaged 9.9 eggs per clutch, whereas 18 others that were 69 mm. or less in snout-vent length, and that must have been mainly or entirely newly matured adults in their first breeding season, averaged only 7.8 eggs per clutch.

Smith (1946:350) states that in the northern part of the range of this skink there is some indication of decrease in size of clutches. This is not well shown by published records. For the southern states, most of the published records of clutch size are by authors who did not clearly distinguish between the three kinds of five-lined skinks, and there is some doubt as to which species is involved in each record. For 56 clutches reported upon from north of approximately latitude 37°, I obtain a slightly higher figure than for 11 clutches from south of this line. Geographic trends are, of course, obscured by individual variation, and perhaps by abnormal clutches produced by individuals kept in captivity.

In Table 7, the figures marked with asterisks pertain to clutches that might have belonged to skinks of the species *E. laticeps* or *E. inexpectatus* since they were recorded in regions where *laticeps* and in some cases, *inexpectatus* also, occurs along with *fasciatus.* If these questionable clutches are excluded the remaining 55, definitely of *fasciatus,* average 8.48 eggs per clutch, whereas the 12 questionable clutches average 8.42. Both figures are close to the average of 8.82 ± .32 eggs for the 34 natural nests recorded in the present study. For the total of 1661 eggs of 182 clutches, from the combined sample of all available records for clutches found in the present study or reported upon in the literature, the average egg number is 9.13.

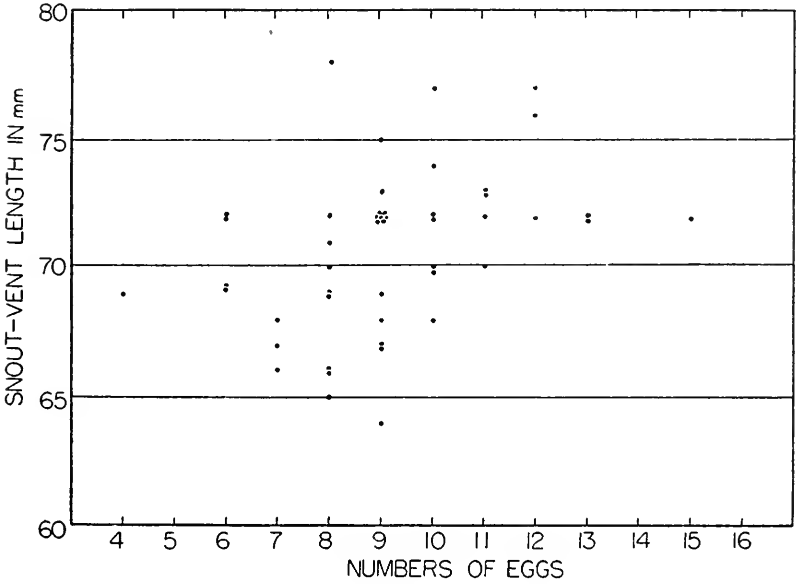

FIG. 10. Correlation between size of female and number of eggs in clutch; females in their first breeding season, mostly less than 72 mm. in snout-vent length, produce smaller clutches, on the average, than do larger and older females, but there is extensive overlap.

To sum up the available information on clutch size, the number of eggs is most typically 9, 10, or 11 and is more in large old females, than in small, newly matured females. In natural nests, even in those that are successful, there is often some loss of eggs, which are eaten by predators, or by the female herself, with the

TABLE 7.—NUMBERS OF EGGS PER CLUTCH, TIME OF OCCURRENCE, LAYING DATES AND HATCHING DATES, AS REPORTED IN THE LITERATURE BY VARIOUS AUTHORS.

AUTHOR	Numbers of eggs per clutch	Date recorded	Natural nest	Laying date	Hatching date	Locality
Allard	7*	...	Yes	...	...	Northern Georgia
Bishop	8*	...	Yes	...	...	Breathitt Co., Kentucky
Blanchard	9*	...	...	...	...	Tennessee
Burt	6; 11	May, and June 18, 1926	Yes	June 12, 1926	...	Douglas Co., Kansas
Burt	9*, 9*, 9*, 10*	June 25 to July 13, 1926	Yes	...	...	Arkansas
Burt	8*	June 6, 1933	Yes	...	...	Ashville, North Carolina
Burt	8*	June 28, 1934	Yes	...	...	Scott, Mississippi
Burt	6*	July 7, 1933	Yes	...	...	Emma, Georgia
Burt	6*	July 8, 1933	Yes	...	...	Elk River, Alabama
Cagle	Average 9.16 in 26 nests (6-15)	June – July	Yes	June 30	July 23-24	Elkville, Illinois
Conant	7, 9, 10, 11, 13	...	...	...	July 27, July 27	Ohio
Dunn	12*	...	...	...	Aug. 9	
Evans and Roecker	6, 7	...	Yes	...	First week of Sept.	Arden, Ontario
Fitch (field notes)	9	July 22, 1947	Yes	...	...	Vernon Parish, Louisiana
McCauley	3; 20 in 3 other nests combined	...	Yes	July 5 and 6	August 30	Maryland
Noble and Mason	2, 5, 5, 6, 7, 8, 8	...	No	May 23, 27, 31; June 6, 6, 13, 20	July 5, 5, 6, 7, 9, 17	Anderson Co., Kansas
Ruthven	6, 6, 8, 9, 11, 13, 14	...	Yes	...	...	Michigan
Smith	9	...	Yes	...	...	Ohio

result that the egg counts made by various observers average somewhat lower than the numbers actually produced. The loss during incubation cannot be measured readily since it is almost certainly sharply increased by the disturbance entailed in observing nests. Exposing nests, even momentarily, for observation, may result in compacting of the surrounding soil, desiccation, temporary or permanent desertion by the female, and exposure to predation. Some indication of the incidence of loss during incubation might be obtained by counting and measuring the eggs in newly found nests and correlating numbers with size (indicating the length of time incubated).

BROODING

Lizards and snakes of several different families, are known to brood their clutches of eggs, although the great majority of oviparous forms do not do so. The brooding habit is perhaps best known in *Eumeces fasciatus,* and has been described by many authors. By far the most thorough account is that of Noble and Mason (1933) who observed and experimented upon seven females that laid clutches of eggs in captivity. These females, kept in separate terraria, excavated nest burrows for reception of their clutches, and remained with them throughout the time of incubation. There were three characteristic brooding postures; curved in a semicircle around the clutch, in an S-shaped figure extending among them, or lying straight, either over or among the eggs. The brooding females, taken quietly from their nests without disturbing them, were found to have temperatures averaging .4° C. higher than the nests. Evidently normal room temperatures were maintained in the laboratory where the terraria were kept. The females occasionally left their nests, especially in late afternoon, to wander about the terraria, and to bask in sunlight. While basking, their temperatures averaged 2.7° C. higher than the nest temperatures. The authors suggested that an important function of the brooding female was to transfer warmth from absorbed sunlight to the eggs. They state: "In nature the importance of the mother's body heat in the incubation of the eggs probably varies greatly with the type of nesting site selected." They suggest that in clutches deposited in logs or stumps beneath a thin layer of bark exposed to direct sunlight the need for warming by the female would be less.

My own observations do not support the idea that brooding by the female serves to hasten the development of the eggs. Both in the laboratory and in natural nests, clutches deserted by disturbed females hatched and the hatching was not unduly delayed. In the field, females were never observed to bask in the sun beside their nest burrows, and seemingly left them infrequently even to feed. When a female was caught in her nest burrow, her temperature nearly always approximated that of the surrounding earth with which she was in contact. The temperature in each nest depends primarily upon its situation. When the immediate vicinity of the nest receives direct sunlight, the eggs are warmed without the aid of the female, but when there is no sunlight the temperature is much lower. In order to maintain an appreciably higher nest temperature the female would have to make frequent trips to spots perhaps several feet or several yards away to find sunlight. Upon returning to the nest, her body heat would be quickly dissipated into the eggs and the surrounding damp soil. She would need to shuttle back and forth almost continually between the nest and a spot exposed to sunshine. Cloudy weather often preventing the warming of the eggs by absorption of solar heat prevails during much of the incubation season, in the region of the present study, and probably to an even greater extent throughout the range as a whole.

Noble and Mason state (*op. cit.*:9) that while in some non-brooding kinds of lizards the eggs are actually damaged by turning, the female *fasciatus* frequently turns her eggs and moves the whole clutch about in the nest cavity. On returning to their nests the experimental females each invariably touched one or more eggs with their tongues as an olfactory test. Eggs of other kinds of lizards not of the genus *Eumeces,* and shellacked eggs of *fasciatus*, or paraffin models of them, ordinarily were discarded immediately after a single touch of the tongue. Eggs of other individuals of the species, and even the eggs of *Eumeces laticeps* were accepted as part of the brood. Any of the experimental females would quickly retrieve one of her eggs moved a short distance outside the nest cavity. Even if the whole clutch of eggs were scattered about, the female would, over a period of hours, gather the eggs and return them to the nest cavity. This movement of the eggs is accomplished by rolling or pushing them in a loop of the body or tail, or, less frequently, by grasping an egg in the jaws, lifting it, and gently placing it in a new position. Even if the females were blindfolded, they were still able to retrieve scattered eggs, but one in which the tongue tip was experimentally removed showed no further interest in its eggs, presumably having lost the capacity to recognize them by olfactory test.

In the present study clutches unattended by females were observed to sustain heavy losses, both in the laboratory and in the field, and no doubt the attending female performs important functions other than that of warming the eggs. In the damp or wet nest cavity, the eggs tend to adhere to each other and to the earth walls and floor, and become sealed to such surfaces as a result of partial drying, reducing the amount of surface exposed to the air and probably hindering respiration. An eggshell sealed in prolonged contact with the soil tends to rot with the result that it is easily ruptured, and even if it is not broken there is the likelihood of fungi or microorganisms gaining entry and killing the embryo. In many of the eggs that were handled to obtain measurements and weight, rupturing of shells occurred. The shells are tough and elastic to the extent that even when eggs being handled were accidentally dropped on the floor on several occasions, no damage to them resulted. However, slight friction on the shell was sometimes sufficient to puncture one. Particles of sharp rock from the nest cavity may adhere to the shell, and result in rupturing, perhaps at weak spots where prolonged contact with the soil has caused deterioration. The female tends to keep her eggs in a compact cluster, shifting their position frequently so that no part of an eggshell adheres to its surroundings long enough for rotting to occur, and most of the surface of each egg is exposed to the air.

Another important function of the brooding female seems to be that of altering the nest burrow and shifting the eggs so that the effects of unfavorable weather are minimized. The usual response to warm and dry weather is deepening of the nest burrow. A cavity originally in loose soil on the underside of a flat rock, having the eggs in contact with the rock surface, may be displaced downward. The female excavates loose soil from the floor of the burrow and packs it on the top and sides, until the eggs are two or even three inches underground, in a cavity different in position and shape from the original one, although derived from it by gradual stages. In many instances, however, no such response to drying was observed. Probably extensive alteration of the nest burrow no longer is possible after drying of the soil has progressed beyond a certain stage as these skinks are not strong diggers. In some nests that were examined frequently, with resulting desertions by the attending females, the outlines of the cavities became indistinct and the soil around them became dry and packed. In heavy rains, when nest burrows are partly flooded, the females move the eggs to avoid their being submerged. The extent of the female's activity within the nest burrow is suggested by the glazed condition of the earth walls and floor, and by the mottled appearance which the eggshells soon acquire as a result of being slid and dragged about in the nest cavity.

Still another important function of the female is to dampen the nest burrow to prevent desiccation of the eggs. Even in dry weather, females taken from nests almost invariably voided water in relatively large quantities. They drink dew or other available water, and may void the contents of the bladder to moisten the nest cavity, as on numerous occasions, when nests were exposed by raising flat rocks covering them, part of the chamber was seen to be recently watered, and distinctly moister than the surrounding soil.

Noble and Mason (*op. cit.*:16-19) found that brooding females, in the laboratory, would vigorously defend their eggs against small enemies, including mice and lizards and the smaller kinds of snakes that were tested. The female watched alertly as the intruder approached, and attempted to bite it if it came too near or touched an egg. The females failed to defend their nests against persons and against a large blacksnake; when confronted with such a threat, the female would run from her nest cavity to hide. Cagle (1940: 228) stated that the brooding females found by him stayed in the nests even when the logs in which they were situated were chopped open with an ax, and that the skinks would attempt to bite when touched with the finger.

In the present study, females whose nests were exposed never made any active attempt to defend them. Many darted away and hid as soon as they were exposed. In other instances, especially when the nest cavity was only partly exposed, from one side, the female cowered back against the inner wall, opening her mouth in threat if closely approached. If further molested she might then attempt to escape. In brooding females a tendency to sluggishness, and an affinity for the eggs delayed the usually speedy escape reactions. The temperature of the female was ordinarily lower than it would have been in the open or on the underside of a flat rock, and this also tended to slow her reactions. Gravid females when exposed in nest cavities that still contain no eggs are similarly sluggish and reluctant to leave differing little or none in behavior from those that have laid their clutches. Usually the female was found with her body encircling the eggs, holding them together in a compact cluster in the center of the nest cavity. The eggs rest in contact with the loose soil on the floor of the cavity, with each other, and with the female's body in the case of the outer ones of the cluster.

Normal brooding habits proved to be difficult to follow because the females were easily disturbed. In many instances those that had excavated nest burrows, but had not yet laid, deserted the nests after the disturbance involved in raising the sheltering rock. Females that had already laid before discovery of their nests were somewhat less inclined to desert, but many did so.

On numerous occasions, at the time of year when most females are gravid and are staying in nest burrows, I have discovered well formed nest burrows empty and seemingly deserted, with no female in evidence nearby. In some instances the female may have been out foraging or basking although she was not seen, and in other instances the female may have been killed by a predator or eliminated by some other accident. However, it seems that gravid females frequently do desert their original nest burrows, for one cause or another, and excavate new ones. Such desertions were noted many times in the females observed on the study area, where the disturbance from my own activities in raising the sheltering rocks may have caused shifts, but it was probably not the sole motivation. One female shifted approximately 120 feet, to excavate her second nest burrow in a site that was damper and more heavily shaded than the first site. This was in the notably dry summer of 1952. Most of the favorite sites under flat rocks in open situations, that were used in 1950 and 1951, were not occupied in 1952 or 1953, although several females did use them for original excavations, which were deserted before laying, as drought conditions developed. In the summers of 1952 and 1953 nests were difficult to find, and those discovered were on the average deeper and better protected than those found in other years.

As compared with other North American lizards in general, *Eumeces fasciatus* is notable for the relatively exposed and superficial situations chosen as nesting sites. However, it occurs in a climate of high humidity; in contrast, the great majority of our lizards live in arid climates where the eggs are in much greater danger of desiccation, and require better shelter to maintain the humidity at a sufficiently high level. Accounts in the literature and observations in the present study indicate that these skinks exercise a wide range of choice of nesting sites. Ruthven (1911:264) stated that in northern Michigan nests were usually in decaying logs; occasional nests were found in burrows in sand, but invariably decaying wood was present in or around at least part of the nest.

Blanchard (1922) mentions a nest in Tennessee that may have been made by either this species or *E. laticeps* "in a hollow in a dead willow tree about fifteen feet from the ground buried in the loose, damp, rotted wood." Noble and Mason (*op. cit.*:16) quote Blanchard (*in litt.*) that in northern Michigan *fasciatus* nests in logs that are exposed to sunlight. Conant (1951:31) stated that several clutches of eggs found in Ohio were an inch to six inches beneath the upper surface of the log or stump which sheltered them. Evans and Roecker (1951:70) record finding two incubating females inside rotten pine logs, in Ontario. Cagle, studying this species near Elkville, Illinois, in oak-hickory woods, found 25 natural nests of which three were in loose soil among the roots of a fallen tree, another was under loose bark of a log, and the remainder were all in cavities of partly decayed logs. Bishop (1926:119) recorded finding a female with a clutch of eggs beneath damp boards at Quicksand, Breathitt County, Kentucky.

In the present study, more than one hundred natural nests were found, of which just one (containing two clutches of eggs) was in decaying wood beneath the bark of an old log. All other nests were beneath rocks. On the University of Kansas Natural History Reservation, where most of the nests were found, the policy is not to tear apart decaying logs; therefore the nests probably present in such situations were not ordinarily found. On several occasions groups of hatchlings were seen on logs within which they probably had hatched. In the area of the study, however, decaying logs are scarce. The hardwood forests consist mostly of young trees that are second growth on cutover areas or pioneer on areas that were previously grassland. Because of frequent cutting there are few old mature trees, and logs have not accumulated on the forest floor. In northeastern Kansas, nesting in logs is comparatively rare. On wooded slopes and the edges of level hilltops, the flat limestone rocks that are often abundant provide preferred nesting sites. Even on collecting trips off the Reservation, where stumps and logs could be torn apart and searched, flat rocks were found to provide the main source of nesting sites. These nest rocks varied from less than an inch in thickness to nine inches or more, and from a few inches in diameter to three feet or more. Some were resting loosely on the surface of the soil and others were deeply sunken, on one side. Some were in situations exposing them to nearly the maximum amount of sunshine whereas others were in sites nearly always shaded. The varied character of the nesting sites chosen demonstrated a wide range of tolerance for temperature, moisture, and other factors, in the gravid and brooding female and in the developing embryo.

As already mentioned, Noble and Mason (*op. cit.*:9-10) noted that females would accept and brood the eggs of other individuals just as readily as their own, and several writers have reported gregarious nesting habits, with two or more females occupying either the same nest cavity, or separate cavities that were in close proximity. For instance, Cagle wrote that among the small logs he found to contain nests, four logs each contained one nest, five each contained two nests, and two each contained three nests, while three other nests were found within an eight inch square area in loose soil among tree roots. McCauley (1939:93) in Maryland found three females brooding clutches of eggs, which totaled 20, and which were so near together that there was uncertainty as to which clutch certain eggs belonged in.

The gregarious nesting habit may be of benefit in permitting maximum utilization of choice nesting sites, where such sites are in short supply in an environment otherwise favorable. Also, the gregarious tendencies make possible more continuous guarding of the eggs against such natural enemies as can be repulsed by the female, since each female occasionally interrupts her brooding to bask or forage.

Many of the nests that I found were in close proximity to others. Often two nests, and sometimes even three, were found beneath the same rock, and sometimes a distance of only two or three inches intervened between the separate clutches. It seemed, however, that in almost every instance each female had excavated a separate nest chamber originally. In some instances adjacent nest chambers communicated with each other.

On July 13, 1948, a communal nest was discovered beneath loose bark of a decaying elm log. There were 22 eggs in the combined clutch, and there were two females in the vicinity. The bark was raised on several different days to examine the eggs, and one or both females always were found with the eggs.

On June 10, 1949, at the pond rock pile, a flat rock was turned and an unusual nesting aggregation consisting of a minimum of eight females, and probably more than ten, was found. The nests were somewhat disturbed by movement of the rock. The ground beneath was honeycombed with tunnels connecting the flask-shaped nest cavities, which were in part open to the rock surface on their upper sides. Clutches of eggs numbered 13, 12, 11, 8, and 6 (the last attended by a female which appeared to be still distended with several more unlaid eggs). Of five other females taken, two had laid and three were still gravid. Of the five clutches, two had eggs noticeably larger than those in the other three, and with their shells mottled brown from adhering earth. These nest cavities were about half an inch deep and two to three inches wide. The females were released as soon as they had been examined. One female moved about over the nest areas exposed, and evinced interest in a lone egg which had become separated from the others. She moved up to it, standing high off the ground, with her head turned at right angles to her body as if preparing to push the egg forward in the angle thus formed, and tested it with her tongue, but then she became alarmed and left the vicinity. The flat rock was lowered over the nests again with a minimum of disturbance.

On July 9, 1949, the flat rock covering the nests was raised again. Most of the eggs had hatched. Two broods of hatchlings were still in their respective nest cavities, and one entire clutch had not begun to hatch although its incubation was nearly completed. Three eggs of *Scincella laterale* were found mixed with the *Eumeces* eggs. One of these was opened to verify their identity; the other two hatched a few days later in the laboratory.

The following selected excerpts from my field notes, setting forth histories of several nests, so far as they were known, give some idea of the types of nesting sites chosen, the behavior of the females, and the hazards to which the eggs are exposed.

No. 1. At corner of pond rock pile.

June 21, 1951. Female escaped when rock was turned. One egg measured 12.5 x 8 mm., mud-stained.

June 22, 1951. Nest not in evidence when rock was turned; digging into loose soil beneath to a depth of about an inch I exposed the eggs but did not disturb them further.

July 23, 1951. When rock was turned, female did not attempt to escape, but withdrew to far corner of nest cavity; when caught she voided a large scat which seemed to consist mainly of *Ceuthophilus* remains. Largest eggs in the clutch were 18 x 10 mm. but two were noticeably smaller, and all were heavily coated with dried mud.

July 30, 1951. Six young in the nest cavity, still not fully active; all of them were heavily coated with dried mud.

No. 2. At hilltop ledge, under flat rock 13 x 10 x 1 inches, with one edge sunken in soil; exposed to sunshine for most of day.

June 24, 1951. Female, snout-vent length 70 mm., tail 27-51, weight 5 gms. Nine eggs, one of which measured 14 x 8 mm.

July 18, 1951. Nine eggs still in their original nest cavity, attended by the female; she escaped into crevice behind the rock. The eggs were in slightly damp soil, and in contact with the undersurface of the rock on their upper sides; one egg was 17 x 10 mm.

July 26, 1951. Eggs caked with dried mud; still attended by female.

July 30, 1951. Dry and empty eggshells in nest cavity, evidently all the eggs had hatched; no other trace of female nor of young; July 28th seems most probable hatching date—if, on the 27th, some of eggs almost certainly would have shown signs of hatching on the 26th when they were examined, and if on the 29th some stragglers almost surely would have remained at the nest on July 30.

No. 3. In small gully, on lower slope in hickory woods, beneath rock 9 x 9 x 1 inches, shaded by trees on south side for much of the day, especially during latter part of morning.

June 24, 1951. The gravid female was deep in nest burrow.

June 29, 1951. When rock was lifted no trace of nest was visible except for slightly disturbed loose soil at the point where it had been. When some of this loose soil was cleared away, nest was revealed, with 11 eggs, mud-stained, approximately 12.5 x 8 mm. The female was cold and sluggish, and did not attempt to escape, but cowered in the back of the nest burrow, with jaws gaping; she was caught and marked.

July 20, 1951. Eight eggs remaining in the nest—two were accidentally destroyed in moving them. These two were fertile and contained live embryos, one of which measured 29 mm. in over-all length. One of the remaining eggs was 16.5 x 10 mm. Female was present with the eggs.

July 25, 1951. Eggs still present in the nest cavity; female not in evidence, but might have been concealed in corner of nest chamber as it was not disturbed.

July 28, 1951. Female was again found with the eggs. One or more of the seven remaining eggs were punctured in moving them during their examination. Eggs about 16 x 10 mm.

August 3, 1951. Female was in nest with the eggs some of which are slightly indented from drying.

August 6, 1951. When rock was turned, female darted out and ran to cover about ten feet away. The eggs had hatched but two young remained in the nest cavity, still rather slow and feeble in their movements and not yet fully active. When routed from cover a second time, the female ran back to the nest rock and took shelter beneath it.

No. 4. On upper slope above ledge, under a rock 18 x 9 inches, in site shaded most of day; burrow nearly concealed beneath rock.

June 24, 1951. Nest occupied by a gravid female, apparently ready to lay.

June 30, 1951. Rock covering this nest has been undermined by a mole tunnel, and many nearby rocks are undermined also. The eggs were almost certainly destroyed by the mole's tunneling and may have been eaten by it, since no remains are in evidence.

No. 5. At hilltop ledge beside old abandoned road, beneath flat rock nine inches in diameter and about 1½ inches thick, shaded for first half of morning and most of afternoon, but exposed to mid-day sunshine.

June 29, 1951. Standing water in bottom of nest chamber 1½ inches below underside of the rock. Some of the eggs are more than half submerged. One egg is 14 x 8 mm.

July 21, 1951. Entrance of abandoned nest burrow has been enlarged by running water channelled through in run-off during and after heavy rains; shrivelled remains of eggs present at the bottom of the burrow.

No. 6. On grassy hilltop a few yards from ledge under flat rock, 9 x 6 x 2 inches.

July 23, 1951. Large female (snout-vent length 75 mm.) with three eggs, 16 x 22 mm.

July 27, 1951. Female escaped from nest cavity as rock was raised. Three eggs were still in the nest, and a young skink was partly emerged from one. A second egg not yet hatching was somewhat flaccid, 16 mm. long, heavily coated with dried mud. The third egg much shrivelled, was opened and found to have a dead fetus, perhaps a week short of hatching.

July 28, 1951. The flat rock which formerly covered the nest cavity was found to have been raised and displaced, and no trace of the female, eggs or young remained. Of possible predators that might have moved the rock and destroyed the nest, skunk and opossum seemed the most likely, but there was no definite clue as to the predator's identity.

No. 7. Two feet northeast of pond rock pile, under rock about one foot square on upper surface with maximum thickness of about eight inches, lying with upper side at 45-degree angle. The nest was under one edge, with approximately three inches of rock over it. The rock was exposed to sunshine throughout the day, except for grass shading its edges.

July 23, 1951. When rock was turned, the female darted out of the nest cavity, but in her dash to escape she dropped into a near-by pitfall. When handled, she voided feces which contained the nearly intact shell of a skink egg. Six eggs present in the nest; one selected as typical was 11½ x 8 mm. The eggs were slightly misshapen and might have been damaged from drying.

July 26, 1951. When rock was raised, female darted out and escaped. The six eggs still remained in the nest.

August 2, 1951. When rock was raised the female was not in evidence, and only three eggs could be found; they had fallen from the nest cavity to the bottom of the depression where the rock was imbedded and were somewhat dried and indented.

No. 8. North slope, beneath rock approximately 18 x 15 x 4 inches, at edge of small gully, where shaded most of the time including mid-day hours.

July 20, 1951. Female attempted to escape from the nest. Four eggs visible in nest, one 15½ x 10 mm.

July 25, 1951. When rock was raised the female ran from the nest.

July 27, 1951. When rock was raised the female was in the nest with the eggs; she ran and hid beneath a boulder five feet away. After a few minutes she emerged and ran 15 feet to a hickory sapling and climbed it.

July 28, 1951. Female was not in the nest but the four eggs were still present.

July 30, 1951. Female found dead and partly eaten by ants beside rock one foot from nest; eggs still present in the nest.

July 31, 1951. Eggs still present in the nest.

August 3, 1951. Eggs still present, including some deep in the nest cavity which apparently were overlooked previously.

August 6, 1951. One much indented egg found outside the nest cavity was opened and found to contain a live fetus, seemingly fully developed and normal. The opened egg was placed on damp soil in a shady place near the nest, but two hours later the hatchling had been killed and partly eaten by swarms of ants.

August 9, 1951. The remaining eggs had disappeared, evidently taken by a predator as no empty shells remained to indicate that the young had hatched.

HATCHLINGS

Cagle (1940:229 and 232) has graphically described and illustrated the hatching of the five-lined skink, and numerous observations in the present study have served to corroborate his description. The first indication that the time of hatching is at hand is a twitching or jerking movement within the egg which continues until the shell is slit. According to Noble and Mason (1933:5) the shell is slit with the elongate premaxillary egg tooth which has its distal third bent forward nearly at right angles to its base. Some young remain for an hour or more with only the snout visible, however, once the head is extruded it is not again withdrawn unless the lizard is badly startled. The eyes are opened and blinked slowly, closed for a few minutes, and opened again. After the eyes have become adjusted, the fore-body emerges and the front legs are freed. In one clutch, observed by Cagle, hatching time for individual eggs varied from 45 minutes to five and three-fourths hours. If startled by visual or tactile stimuli, the little skink may lunge forward through the slit shell, with a sudden straightening of its body, and rush away for several inches. Its movements are slow, stiff and clumsy as compared with those of a skink that is a few days old and fully active. Hatching of a clutch ordinarily extends over 24 hours or more. Some of the young may be fully hatched and active before others from the same clutch have slit their eggshells.

Eggs ready to hatch ordinarily weigh somewhat more than one gram, up to at least as much as 1.7 grams, but much of this weight is made up of water absorbed during incubation. The hatchlings usually weigh from .2 to .45 grams. For each of two eggshells recently vacated, that were washed and squeezed dry, weights were approximately .125 grams. Hatchlings of the same brood differ perceptibly in size with several per cent variation in total length, and weight. Some seem to be less fully developed than others. On July 8, 1952, hatching of the last young in a clutch was observed. Upon emergence, it differed in appearance from the others of the brood hatched a few hours earlier. The top of its head bulged slightly as in fetuses. The umbilicus was not yet closed, and the protruding yolk mass hindered the hatchling's movements and made crawling difficult. In order to progress it had to stand high off the ground to prevent its ventral surface from dragging. Protrusion of the yolk mass has been described in newly emerged hatchlings for the closely related *E. anthracinus* (Clausen, 1938:3-7) as well as in *fasciatus*. Cagle (*loc. cit.*) states that the mass of yolk is at first about 3 mm. in diameter, but is completely used at the end of the third day. A group of young retained by him, without food, died the sixth day after hatching, seemingly from starvation. Three of five recently hatched young were found by Cagle to have eaten ant pupae placed in a box with them on the preceding day, even though the skinks still retained the yolk masses. One hatchling of this group ate its own tail that had been broken off in handling. Cagle described a color change taking place during the first few hours after hatching; the ground color, dull greenish at first, darkens to an iridescent black, the pale stripes are altered from an original tan color to bronze, with a tinge of reddish on the head, and the ventral surface which is partially transparent showing the outlines of the internal organs at first, soon becomes opaque white.

Contrary to the statement by Noble and Mason (1933:5) that in captivity the hatchlings seldom stayed together more than a few hours, litters of young fully active, a day or two after hatching were found in the nests with the females still looped around them on several occasions. On one such occasion, although the brood scattered immediately into surrounding vegetation where they hid, I succeeded in catching the female and six of the young, and put them all together in a nylon bag to carry them back to the laboratory. Several hours after the bag had been placed on a table it was noticed that the family had again gathered into a compact cluster in the bag with the female's body looped around the young in the characteristic brooding position seen in those with young or eggs in their nest cavities. When hatching is complete, the female may leave before the young have dispersed. On August 5, 1950, a nest under observation was found to have all of the young or most of them still clustered in the cavity, but the female was not in evidence. The young were active, and immediately took alarm as the rock was raised exposing them. Almost instantly, they scattered and vanished. Subsequent search revealed five of the young, each poorly concealed in tufts of grass or under dry leaves or other ground litter at the edges of the depression where the rock had lain. Once hidden, these young were reluctant to run again and depended on concealment.

Having once left the nest, the young probably do not return to it, as many nests examined within a few days after hatching were never found occupied either by females or young after their original dispersal. As soon as the dispersal occurs family ties are permanently severed. On July 19, 1950, a group of active hatchlings was observed moving about over a log, on what was probably the first day of activity away from the nest. The log was in the bottom of a steep-walled gully, where it had come to rest the night before. It had been an erect but dead and partly undermined snag on the edge of the gully, and was blown down that night in a violent thunderstorm. Most of the log was held clear of the rushing water in the bottom of the gully by projecting limbs. The little skinks were darting in and out of holes and crevices in the log, pausing frequently to bask. As many as four were in sight simultaneously, but probably the total included several more, as it was difficult to keep track of individuals. An adult female, presumably the mother of the litter was also present, but she took no interest in the young, and they showed no evidence of dependence on her. On the contrary, several times when one or another of the young happened to come near the female in the course of its wandering, and noticed her, it was seen to shy away in sudden alarm.

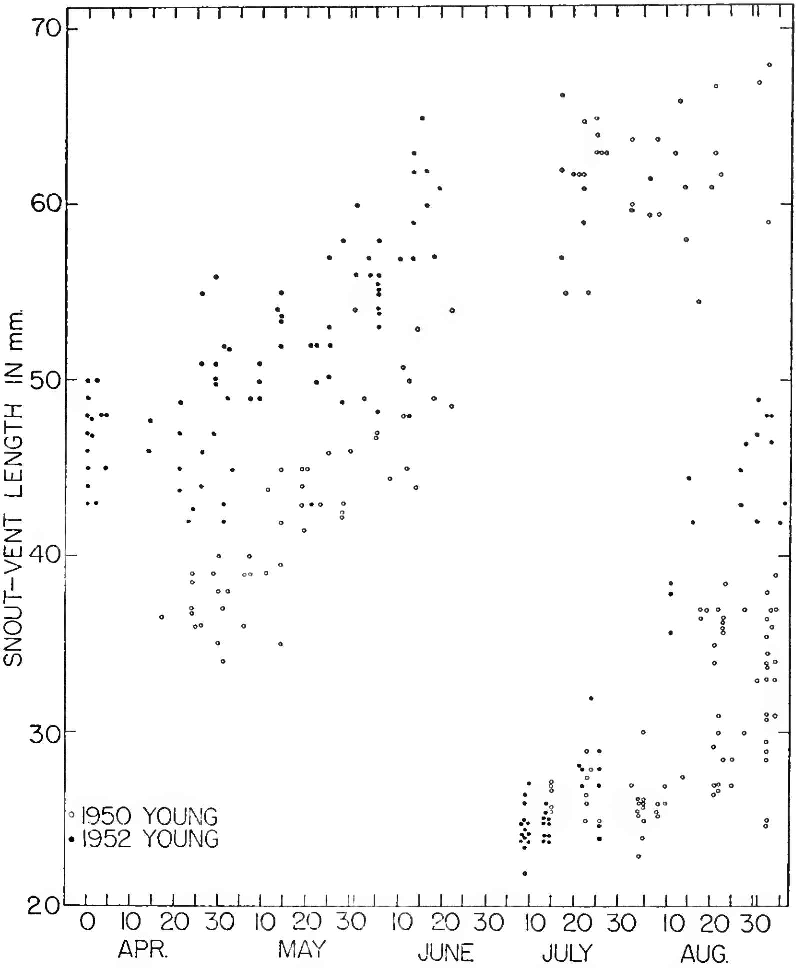

FIG. 11. Sizes on specific dates of young hatched in 1950 and 1952. Approximate size ranges at different times of year, and differences in trend between the two years are brought out.

The young were much more active than the female. These and other young observed in the open were almost constantly in motion. Pauses to bask at any one spot were of only a few seconds duration. A certain log in Skink Woods evidently was the site of one or more successful skink nests each year that observations were made, although a nest was actually found in it only in 1948. On July 26, 1950, recently hatched young were active on this log. Temperature was about 22° C. and the young were alternating frequently between shade and sunshine to maintain their body temperature. Collectively they seemed to cover every square inch of the log surface, poking and probing into niches, crevices and insect borings. They had a tendency to seek out the highest points on the log as resting places.

In moving about, foraging or sunning, the young often carry the tail arched high, and keep it in motion with slow squirming undulations. These undulations may be continued even when the lizard itself has come to rest momentarily. The movements of the tail together with its vivid blue color serve to attract attention to it. Such behavior has not been observed in adults or partly grown young. Jopson (1938:90) observed an instance in which two dogs cornered a young five-lined skink (either the present species or *E. laticeps*) but were distracted by the wriggling of its bright blue tail "either dropped by autotomy or knocked off" so that the skink itself was allowed to escape. On another occasion these same two dogs attacking an adult male skink, were not distracted by the wriggling but dull colored broken tail, and they killed the lizard.

GROWTH

The subject of growth in *Eumeces* was briefly discussed by Taylor (1936:66) in his revision of the genus. Sorting fairly large series of museum specimens into seeming age-size groups, Taylor concluded that skinks require as much as 9 or 10 years to attain adult size. For *fasciatus,* for instance, the snout-vent length of 65.7 mm. (small adult size) was considered typical of individuals in their ninth year of life, with yearly gain of only 6 or 7 mm. in length in the young. I have seen the original data on which this conclusion was based, and the age groupings, as assigned by Taylor, seemed plausible. However, in the light of present knowledge, it is certain that the seeming intervals between his assumed age groups would have disappeared with a still larger series of specimens. The eight or nine size groups that Taylor recognized as distinct annual age groups actually comprise only two age groups, each having such wide dispersion of individuals (by retardation of some and acceleration of others) that there is overlapping in size between them.

Growth in reptiles is now much better understood. Many species have been studied by a variety of methods, including observation of growth in captives, recording of growth in marked individuals living under natural conditions, and sorting of large series into age-size groups. Two species of *Eumeces* have been studied in some detail. Breckenridge (1943:601-602) marked all the individuals of *septentrionalis* that could be found in a small colony in Minnesota and he concluded from the growth recorded in several that were recaptured, that these skinks grow to mature size (65 mm. and larger) at the end of their second year of life and are ready to breed the following spring. Rodgers and Memmler (1943:61) plotted the size distribution of a large year-round collection of *skiltonianus* from near Berkeley, California. They found that in this species hatching occurs in July and August, hatchlings are about 25 mm. in snout-vent length, and grow to about 50 mm. by the time they are one year old, and to about 65 mm. at two years of age, but most of them breed at the end of their third year. Within the genus the species *septentrionalis* and *skiltonianus* belong to groups separate from each other and from that including *fasciatus*. While *septentrionalis* and *skiltonianus* resemble each other in their growth pattern and in the time required to reach sexual maturity, *fasciatus* is notably different in its more rapid growth and the shorter time it requires to reach breeding maturity. This would scarcely be expected, as all three are of similar size. Furthermore, *skiltonianus* in the region of Rodgers' and Memmler's study has a longer growing season than *fasciatus* in northeastern Kansas, while *septentrionalis* in Minnesota has a growing season markedly shorter than either. It is noteworthy that each of these three skinks is the northernmost lizard in the section of the country where it occurs.

In the present study growth was investigated by measuring and marking large numbers of young, many of which were recaptured for subsequent records, and by sorting into age-size groups all available measurements. An understanding of the latter set of data was facilitated by correlating it with the growth records of marked individuals. Changes in the phenology of growth from year to year according to weather conditions were noted.

As already indicated, hatching occurs from early July to mid-August in northeastern Kansas. Unseasonably cool weather with frequent rains may cause cumulative delay in breeding and incubation so that hatching may average several weeks later than it does in years with relatively warm and dry weather during the breeding season. Within any one year hatching time is concentrated, so that the majority of the young hatch within a period of two weeks, but microclimates in the situations where the nests are made may differ enough to cause this much spread. Individuals living on north slopes in thick woods, and receiving the minimum amount of sunlight may have their emergence from hibernation and attainment of breeding condition delayed. Later, nesting in the same situations, they may have incubation of their clutches similarly delayed.

Newly hatched young average just under an inch in snout-vent length (23-27 mm.) and weigh .2 to .45 grams. Most rapid growth occurs in the period of weeks following hatching. The growth rate during this late summer period cannot be well shown by comparing average size of series taken on successive dates, because each series is likely to include some newly hatched young.

In 1949, a series of recently hatched young averaged 26.7 mm. on July 10. By August 26, average length in a series collected was 42.9 mm., indicating an average gain of at least .35 mm. per day. One that may be considered typical was marked on July 23, 1950, soon after hatching, and it had a snout-vent length of 26.5 mm. and weighed .25 grams. It was recaptured just a month later when it had grown to 36 mm. snout-vent length, and weighed .8 grams. Potential growth rate under favorable conditions is shown by the fact that some individuals have attained a snout-vent length of 50 mm. by the third week of August, thus approximately doubling their hatching length. A maximum growth rate of about .5 mm. per day is indicated for these accelerated individuals, but on the average, young are considerably less than 50 mm. in length even when they enter hibernation. At the other extreme, representing retarded growth, is an individual having a snout-vent length of only 34 mm. on May 1. It must have been approximately nine months old on that date, but of course had spent at least six months in hibernation. Even if it made rapid growth subsequently, this yearling could scarcely have attained by midsummer the pre-hibernation length of the most accelerated individuals.

During the growing season following their first hibernation period, the young grow to small adult size in most instances. After emerging from a second hibernation they mature sexually and constitute an important part of the breeding population.

Many of the skinks marked before their first hibernation, as hatchlings, when they were a few days or a few weeks old, were subsequently recaptured as well-grown yearlings or small adults, affording ample information as to the usual growth rate and the extremes of acceleration or retardation that occasionally occur. Records of selected individuals in this group of skinks, marked early in life and recaptured after a hibernation, are recorded below.

TABLE 8. RECORDS OF INDIVIDUAL SKINKS MARKED AS HATCHLINGS (BEFORE THE FIRST HIBERNATION) AND RECAPTURED THE FOLLOWING YEAR. RAPID RATE OF EARLY GROWTH IS SHOWN.

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.	August 8, 1951	23½	30½	.25	Had just hatched when first recorded; second capture was made soon after emergence from hibernation. All three captures within a 50-foot diameter.
	April 28, 1952	39	55+½	1.3	
	June 7, 1952	48	69+1	....	
No. 2.	July 8, 1952	25	25 (broken stub)	.3	
	April 23, 1953	42	17+26	....	
	June 23, 1953	56	22+36	....	
No. 3.	July 16, 1948	26½	37	....	Caught at the same place on both occasions; in a little less than a year this female grew to small adult size.
	July 5, 1949	68	101½	....	
No. 4.	August 23, 1950	36	55	.9	The interval between captures included about two months of active life, plus the hibernation period; caught at the same place on both occasions.
	May 19, 1951	46	69½	1.7	
No. 5.	September 2, 1950	34½	33 (broken stub)	....	Tail broken at first capture; recaptured 40 feet from original location.
	June 12, 1951	45	48+3	2.0	
No. 6.	July 28, 1949	36	56	....	Recaptured 75 feet from original location.
	April 21, 1950	49	83	2.5	
No. 7.	August 31, 1951	38	58	....	All three captures within a 70-foot diameter.
	May 25, 1952	48	82	....	
	June 30, 1952	63½	57+26	....	
No. 8.	August 23, 1950	36	44 (broken stub)	.7	Tail broken at first capture. Capture sites 150 feet apart.
	July 23, 1951	69	37+49	....	
No. 9.	August 23, 1949	39	53½ (regenerated)	....	This male was retarded in growth, being still well short of small adult size as its second hibernation period approached; all four captures recorded within a few yards.
	June 7, 1950	46	70½ (regenerated)	2.1	
	July 23, 1950	58	88 (regenerated)	3.7	
	September 3, 1950	62	91 (regenerated)	4.9	
No. 10.	July 31, 1949	38	23 (broken stub)	....	Capture sites 20 feet apart.
	June 17, 1950	58	43+36	3.6	
No. 11.	August 13, 1949	40	66	....	Approximately a year after its original record this skink was recaptured 80 feet away, still short of small adult size.
	August 8, 1950	63	90 (regenerated)	5.0	
No. 12.	August 19, 1949	42	40 (broken stub)	....	All three captures within a 50-foot diameter.
	June 13, 1950	58½	58+28	4.1	
	July 5, 1950	63	62+31	5.9	

Many other young were not caught and marked until the growing season following their first hibernation, and were recaptured within this second growing season weeks or months after they were originally marked, and after they had made substantial growth. Those recaptured near the end of this second growing season, when they were a year old, or a little more, usually had attained small adult size or were nearing it. Selected records of these yearlings are presented below.

TABLE 9. SELECTED RECORDS OF INDIVIDUAL SKINKS MARKED AS YEARLINGS (AFTER EMERGENCE FROM THE FIRST HIBERNATION) AND RECAPTURED ONE OR MORE TIMES THE SAME YEAR. RAPID GROWTH IS SHOWN.

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.	May 2, 1951	38	53½	....	Capture sites 30 feet apart.
	September 25, 1951	62	25 + 31	....	
No. 2.	May 8, 1951......	39	57	....	Capture sites 150 feet apart.
	August 2, 1951....	60	67 + 25	....	
No. 3.	April 17, 1952.....	39	55	1.1	Capture sites 30 feet apart.
	June 23, 1952.....	57	73 (regenerated)	....	
No. 4.	May 20, 1952.....	45	67	....	Capture sites 15 feet apart.
	May 28, 1952.....	47	71	....	
	June 9, 1952......	53	82	....	
No. 5.	May 22, 1952.....	48½	77½	2.0	Capture sites 10 feet apart.
	July 20, 1952.....	63	106	5.3	
No. 6.	June 11, 1950.....	49	49 (broken stub)	2.4	Capture sites 20 feet apart.
	September 2, 1950	63	63 + 31	4.9	
No. 7.	April 14, 1950.....	47	72	1.9	Capture sites 50 feet apart.
	May 29, 1950.....	50	82½	2.5	
No. 8.	May 12, 1952.....	49	77	....	Capture sites 60 feet apart.
	June 18, 1952.....	61½	98	....	
No. 9.	June 4, 1950	54	89	2.8	Both captures at same site.
	August 1, 1950....	64½	101 (broken stub)	5.7	
No. 10.	June 11, 1950.	49	49 (broken stub)	2.4	Capture sites 20 feet apart.
	September 2, 1950	63	63 + 31	4.9	
No. 11.	June 13, 1949.....	57	68 (regenerated)	....	
	August 8, 1949....	70	37 + 11	....	

Adult skinks can be found in greatest numbers in the breeding season and many of the young that were marked were recaptured as newly matured breeding adults soon after their second hibernation, often still short of average adult size. Selected records of such individuals are presented below.

TABLE 10. RECORDS OF INDIVIDUAL SKINKS MARKED AS YOUNG AND RECAPTURED AS ADULTS.

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.	Male				Probably less than a month old at first capture; at second capture 21 months later and 185 feet away, he had red facial suffusion already somewhat faded as the breeding season waned.
	August 21, 1950	34	48	.7	
	May 30, 1952	69	37+49	....	
No. 2.	Male				
	July 31, 1949	39	64	....	All three captures within a 70-foot diameter.
	August 22, 1949	47	75	....	
	May 19, 1951	73	69 (regenerated)	....	
No. 3.	Male				
	August 5, 1949	36	57	....	Capture sites 10 feet apart.
	May 3, 1951	67	103	5.1	
No. 4.	Male				
	June 16, 1951	44	41 (broken stub)	....	Capture sites 535 feet apart.
	May 28, 1952	63	77 (regenerated)	....	
No. 5.	Male				
	April 12, 1950	45	73	1.9	Capture sites 100 feet apart.
	May 1, 1951	67	17+48	....	
No. 6.	Male				This individual had attained approximately average adult size by the 1951 breeding season; all three captures were within a distance of 90 feet.
	April 12, 1950	46	4+15	1.3	
	August 10, 1950	67	75 (regenerated)	5.3	
	May 12, 1951	71	77 (regenerated)	....	
No. 7.	Male				
	April 30, 1950	48½	78½	2.4	
	June 15, 1950	56	94	2.9	
	May 19, 1951	67	90 (broken stub)	....	
No. 8.	Male				
	May 3, 1950	47	51+4	1.7	Capture sites 450 feet apart.
	May 29, 1951	75	115 (regenerated)	....	
No. 9.	Male				
	June 2, 1949	51	46 (broken stub)	....	Capture sites 90 feet apart.
	May 2, 1950	66½	31½+51	7.0	
No. 10.	Male				
	May 20, 1950	58	92½	4.0	Capture sites within 40 feet.
	June 21, 1950	61	95	4.7	
	August 21, 1950	70	108 (broken stub)	7.2	
No. 11.	Male				
	June 25, 1950	62	100	5.1	
	May 1, 1951	71	113	7.1	
No. 12.	Female				
	April 15, 1950	46½	73½	1.5	Capture sites 160 feet apart.
	May 20, 1951	72	113	....	
No. 13.	Female				
	June 11, 1950	51	69	2.5	Capture sites 20 feet apart.
	May 25, 1951	66	40	....	
No. 14.	Female				
	June 6, 1949	52	47 (regenerated)	....	Capture sites 20 feet apart
	May 20, 1950	68½	69 (regenerated)	7.5	
	June 9, 1950	71	71 (regenerated)	....	

TABLE 10.—*Concluded*

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 15.	Female July 2, 1950...... May 21, 1951.....	 60 74	 100 33 + 35	 4.2	Capture sites 20 feet apart.
No. 16.	Female June 12, 1950..... May 1, 1951......	 57 71½	 83 53 (broken stub)	 3.1 6.4	Capture sites 35 feet apart.
No. 17.	Female June 22, 1949..... May 22, 1950.....	 62 72	 24 (broken stub) 27 + 7	 .... 9.0	This female probably hatched in July 1948 and was nearing adult size when first caught at an age of a little less than a year. By the next breeding season it was an average sized adult; both captures at same site.
No. 18.	Female July 4, 1950...... May 23, 1951.....	 64 73	 30 + 55 31 + 62	 4.3	This female probably was approximately a year old when first caught, and she grew to average adult size by the next spring; both captures at same site.
No. 19.	Female July 5, 1950...... June 14, 1951..... June 29, 1951.....	 61½ 73 74	 92½ (regenerated) 111 (regenerated) 106 (regenerated)	 4.7 8.2 5.0	This female was about a year old when first captured; loss of weight in July 1951 was caused by its laying a clutch of eggs. All three captures were within a 15-foot diameter.

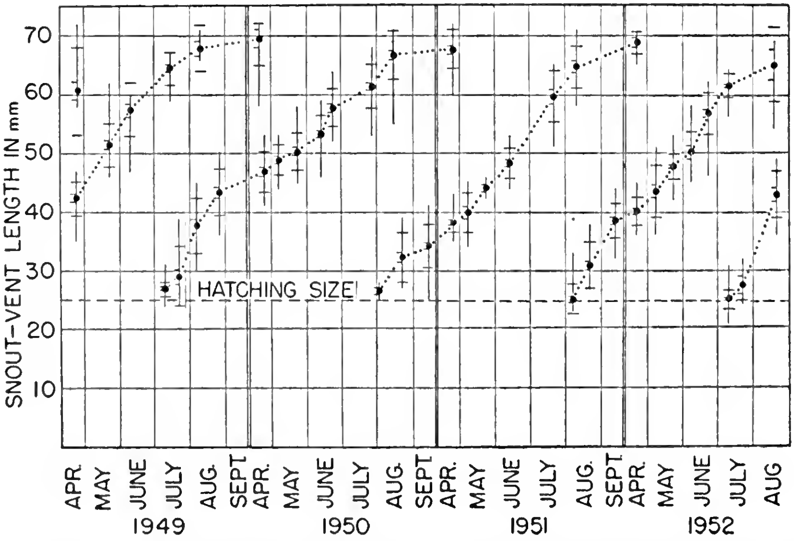

FIG. 12. Sizes of immature skinks of successive annual broods, grouped in biweekly or monthly intervals, with mean, standard error, standard deviation, and extremes shown for each group.

A certain small percentage fail to attain minimum adult size or breeding maturity by the time of emergence from their second hibernation. Among 77 individuals marked as young either soon after hatching or in spring and early summer, and recaptured the following spring, only one had failed to grow to adult size. It was 46.5 mm. in length when marked on June 13. When recaptured on April 25 of the following year, it had grown to a length of 59 mm., still short of minimum adult length. During the interval between captures it had maintained about the average growth rate. Its failure to attain maturity was obviously the result of its early retardation, and probably late hatching was primarily responsible. Although this is the only individual with known history, which failed to attain breeding maturity after its second hibernation, occasional specimens are taken in spring which are somewhat below adult size but seem too large to be young hatched the preceding summer. Obviously, the incidence of such failure from year to year would be influenced by weather conditions, and an unusually cool summer may result in such delayed laying and hatching that an unusually large proportion of young might fail to attain sexual maturity at the usual time. At more northern localities, the percentage of such failures might be expected to increase. At the northern edge of the range attainment of breeding maturity may normally require more than two years. Such delayed development would result in a drastic reduction of the reproductive potential which might be critically limiting to the species, even in an otherwise favorable environment, as the population would be unable to replace rapidly enough the individuals eliminated by normal mortality factors.

In contrast to the delayed development of those that have failed to attain maturity at an age of two years, is the accelerated development of those that have already more than doubled in length before the first hibernation, and continue to grow rapidly after emergence. By late spring they are already approaching adult size, perhaps even before laying has occurred, and while breeding is still in progress. It is certain that in northeastern Kansas there is no breeding by such accelerated individuals approaching adult size at an age of nine or ten months. Farther south in the species' range with a much longer growing season, there is perhaps some possibility of such early breeding by first-year individuals. This would reduce by more than half the length of time required for a generation, and would tremendously increase the reproductive potential. With such added impetus to its reproduction the species might be able to withstand greatly increased predation pressure, or other mortality factors.

Extremes of acceleration or retardation are relatively rare in the population studied. Nevertheless, in April there are some individuals between 50 and 60 mm. in snout-vent length which cannot be classified with certainty as to their age group, and might be either accelerated individuals about nine months old or retarded individuals about 21 months old.

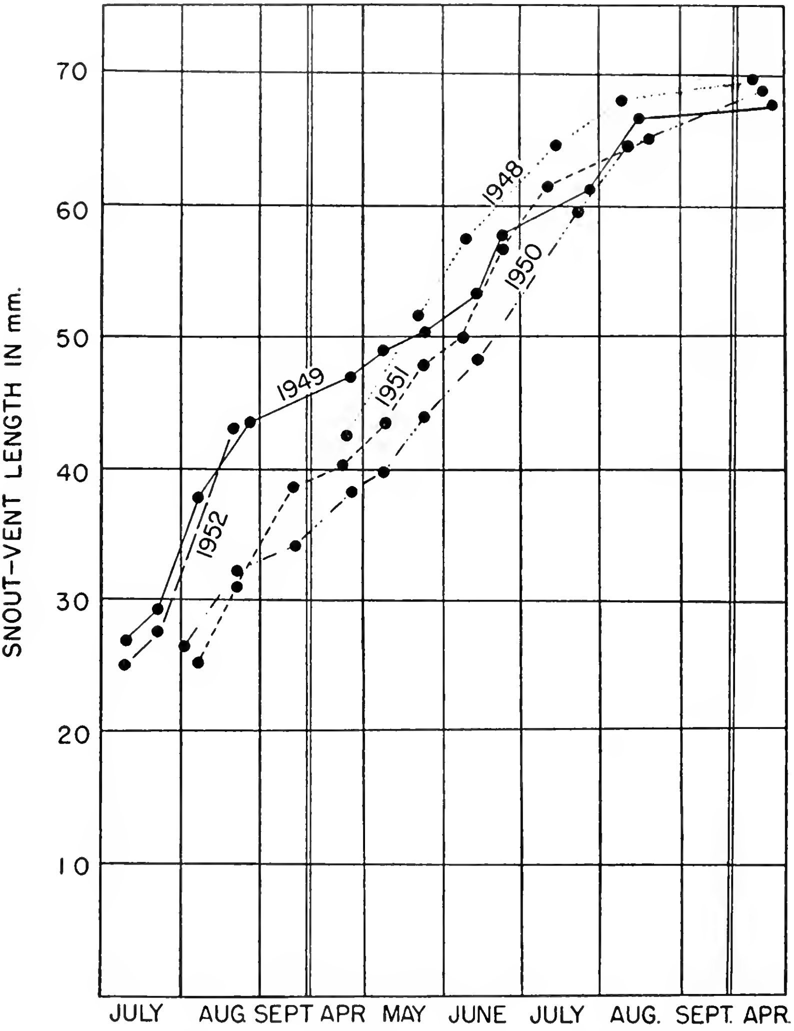

FIG. 13. Growth curves of successive annual broods (designated by the year of hatching), superimposed to bring out differences in trends resulting from changes in weather from year to year.

The spread in size for any given age group is especially large, if data from different years are combined. A typical individual, having a snout-vent length of 25 mm. at hatching in mid-July may have attained 30 mm. by early August, 35 mm. by late August, and 45 mm. by the time it hibernates late in September. Emerging shortly before the middle of April it may grow to 50 mm. by the end of May, 58 mm. by the end of June, and more than 60 mm. by the end of July when it is a little more than a year old. By the time of its second hibernation it may have attained a length of from 65 mm. to 70 mm., and emerges from this hibernation as a breeding adult.

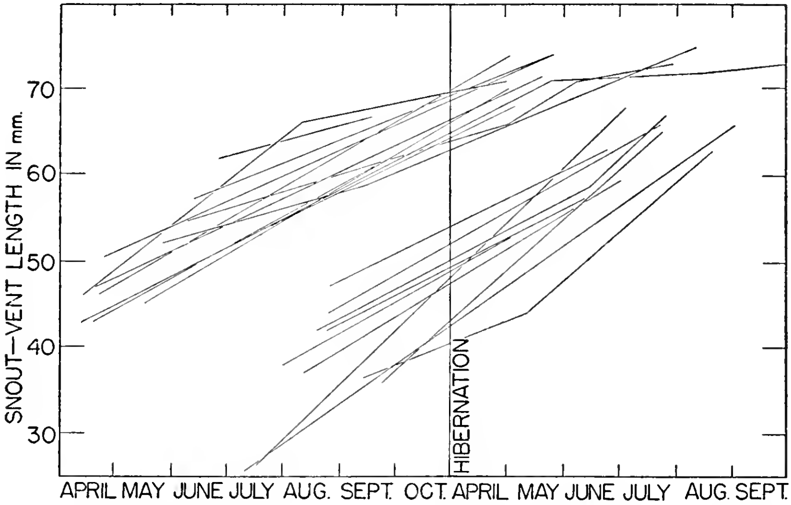

FIG. 14. Records of growth of immature individual skinks, both hatchlings and yearlings, that were marked in one year and recaptured the next.

In reptiles in general there is a wide range in adult size, and the extent and rapidity of continued growth after attainment of sexual maturity and minimum adult size is still insufficiently understood. Information bearing on this problem was obtained in the present study from the recapture of marked skinks already measured as adults. It is evident that the growth rate of the young, amounts to as much as 15 mm. per month in snout-vent length in the late summer period from hatching until hibernation, averages perhaps three or four mm. per month in the summer after emergence from the first hibernation, and tapers off rapidly as adult size is approached.

One hundred of the skinks marked as adults or subadults and recaptured after intervals of months, including, in most instances, one or more hibernation periods, represent in the aggregate, 87 years of growth. These records show that after minimum adult size of 65 mm. is attained, growth slows abruptly, and that by the time a length of approximately 75 mm. is attained in most instances growth has become extremely slow in males and has virtually stopped in females. Males attain a maximum size several millimeters larger than that of females. Individuals differ greatly in their growth, however; some adults continue to grow rapidly till they near the maximum size, whereas others apparently stop growing when they are still below average adult size. Unusually large specimens are not necessarily old, but may have attained their size only a year or two after reaching maturity through the accelerated growth resulting from abundant food and predisposing genetic factors. Likewise, unusually old individuals are not necessarily the largest, but may be only a little above average adult size. It may be assumed that no growth occurs during the period of winter dormancy, which occupies approximately half the year in the population studied. To compute growth rates, in those recaptured after an intervening hibernation, periods of hibernation, arbitrarily estimated as six months, were subtracted from the time elapsed between captures.

TABLE 11. AVERAGE GROWTH RATE IN A SELECTED SAMPLE OF SKINKS OF ADULT SIZE.

SIZE GROUP	Males		Females	
	Average growth mm. per month	Number of skinks in sample	Average growth mm. per month	Number of skinks in sample
65–68 mm.	1.4	11	.8	12
69–72 mm.	.7	12	.4	21
73–76 mm.	.7	13	.3	21
77–80 mm.	.4	7	....	....

Opportunity to compare the rapid growth of young during their first year of life with the relatively slow continued growth after attainment of sexual maturity is afforded by the records of skinks caught and marked while yet immature and recaptured in two or more successive years after their attainment of sexual maturity. The records of selected individuals of this group are presented below. With the exception of number three, all in this series are of the 1949 brood, and probably all hatched within a two-week period.

TABLE 12.—RECORDS OF INDIVIDUAL SKINKS MARKED AS YOUNG AND RECAPTURED REPEATEDLY AFTER ATTAINMENT OF ADULT SIZE, SHOWING TREND OF PROGRESSIVELY SLOWING GROWTH.

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.	Male				At an age of 33 months this male was far short of maximum size, and smaller than some males a year younger; all four captures within a 65-foot diameter.
	April 12, 1950	43	71	1.5	
	August 30, 1950	56	56+21	5.4	
	May 23, 1951	68	59+32	....	
	April 28, 1952	73	62+38	6.6	
No. 2.	Male				At an age of approximately one year this male was approaching small adult size; when last captured at an age of 34 months, he was a large adult. All five records within a 190-foot diameter.
	July 5, 1950	61	92½ (regenerated)	5.2	
	July 28, 1950	64	97 (regenerated)	5.4	
	May 3, 1951	68	96 (broken stub)	5.8	
	June 21, 1951	72	101½ (regenerated)	....	
	May 1, 1952	78	101 (regenerated)	....	
No. 3.	Male				This skink was nearly a year old and nearing adult size when first captured; recaptured in each of the four succeeding years, he showed slowing growth. He was near the maximum size at the time of his last capture when he was about 57 months old, and evidently had stopped growing (for movement see No. 2, p. 110).
	June 22, 1949	65	111	....	
	May 4, 1950	72½	115	7.3	
	June 17, 1950	73	116	7.8	
	May 15, 1951	80	125	....	
	May 13, 1952	82	125	....	
	April 6, 1953	82	104 (regenerated)	....	
No. 4.	Female				This individual, marked when less than two weeks old, had grown to nearly the maximum female size at an age of 34 months; all four captures within a 175-foot diameter. (See Figure 24).
	July 13, 1949	27	34½	....	
	June 1, 1950	54½	93½	3.1	
	August 21, 1951	74	119	....	
	May 1, 1952	76	123	10.0	
No. 5.	Female				All six records within a 65-foot diameter (See Figure 21).
	April 15, 1950	43	70	1.4	
	June 5, 1950	52½	87	2.8	
	May 25, 1951	71	82+29	....	
	September 28, 1951	73	111 (regenerated)	....	
	April 26, 1952	74	113 (regenerated)	7.4	
	April 24, 1953	76	114 (regenerated)	....	
No. 6.	Female				Hatched in July 1949, this skink had attained the maximum female size at an age of a little more than three years; (for movement see Figure 25).
	April 21, 1950	46	75	2.1	
	May 7, 1950	48	15 (broken stub)	2.0	
	May 3, 1951	74	29+57	8.5	
	May 2, 1952	78	25+64	....	
	August 27, 1952	79½	95 (regenerated)	8.3	
No. 7.	Female				Hatched in July 1949, this skink was 11 months old and about half-grown when it was marked. When last caught at an age of 35 months it was of average adult female size, having grown less than numbers 4 and 6 at the same age. All five captures were within a 60-foot diameter (Fig. 24).
	June 5, 1950	51	82	2.5	
	July 13, 1950	59	93	3.9	
	July 29, 1950	64	98	4.4	
	August 21, 1951	69	80 (broken stub)	5.0	
	May 28, 1952	73	83+9½	....	

TABLE 12.—*Concluded*

	Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 8.	Female				Hatched in July 1949, this skink was of average adult female size and was breeding in May 1951; it grew nearly to maximum female size in the next 11 months. All captures within a 70-foot diameter.
	April 26, 1950.....	50½	78½	2.7	
	May 24, 1951.....	74	107 (regenerated)	....	
	April 28, 1952.....	78	93 (regenerated)	8.5	
	April 23, 1953.....	80	93 (regenerated)	....	
No. 9.	Female				All three captures at the same site.
	July 5, 1950......	60	95	4.5	
	August 6, 1951....	71	106½	5.6	
	May 28, 1952.....	72	110	8.5	
No. 10.	Male				Hatched in July 1949, this male grew less rapidly than most, and in the spring of 1953 was smaller than some others that were a year younger, or even two years younger.
	April 23, 1950.....	46½	66 (regenerated)	1.8	
	June 13, 1950.....	52½	26+3	2.7	
	September 2, 1950	66	32+51	6.2	
	May 29, 1951.....	67	33+58	....	
	August 3, 1951....	70	94 (regenerated)	....	
	March 27, 1953...	74	78 (regenerated)	7.1	
No. 11.	Female				This skink had attained maximum female size when she was a little less than four years old.
	April 26, 1950.....	50½	78½	2.7	
	May 24, 1951.....	74	87	....	
	April 28, 1952.....	78	72+21	8.5	
	April 23, 1953.....	80	73+20	....	

Differences in their growth rates therefore reflect differences in sex, individual vigor, and local situation, in individuals living at the same time and within the same general environment.

Changing weather, and other factors that vary from year to year cause marked differences in the dates of important events in the annual cycle, and in the stage of development at any given date. Data are available for five successive annual broods of young, those of 1948, 1949, 1950, 1951, and 1952, and each brood differs from the others to some extent, as shown in Figures 11 to 13. In 1949, for instance, young hatched relatively early, and probably most of them were active by the middle of July. They made rapid growth in August, averaging larger than young hatched in other years on any given date in late summer. However, they retired into dormancy early in the fall. Cool and dry weather in early September ended their activity for the season. In 1950, young hatched, on the average, at least three weeks later, about the first of August, but they remained active until late in September, and by hibernation time had partly caught up to the stage of development attained by the young of 1949. Most young of 1951 hatched late in the first half of

August, and at first were smaller than those of 1950 and much smaller than those of 1949 on corresponding dates, but favorable weather in the early fall hastened their development. By early September they had caught up and passed the stage of development of young of 1950 and by the time they retired to dormancy in late September, they had reduced by half the size-advantage of the young of 1949 at the time these latter retired into hibernation. The young of 1951 appeared to be few in numbers, and a lack of competition may have been a factor in their rapid early development.

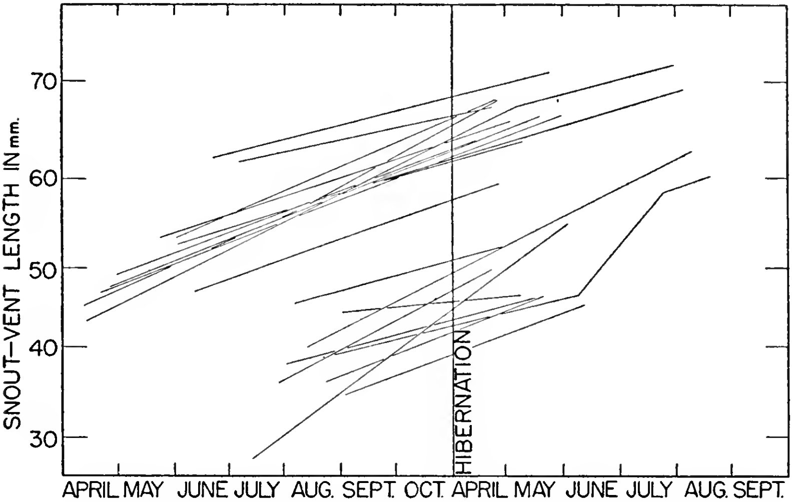

FIG. 15. Records of growth in another group of recaptured young that grew less rapidly than those of Fig. 14.

The young of 1948, first sampled after their emergence from their first hibernation in mid-April of 1949, were then somewhat intermediate in size as compared with those of 1949 and 1950 at the same times of year. Their subsequent development was rapid; by late May they had caught up and passed the stage reached by the 1949 young at the same time of year. The young of 1950 after having a late start, were further set back by cold weather in April 1951 delaying their emergence from hibernation. As a result they were still unusually small in late April and May. Even though they grew rapidly subsequently, they were consistently smaller than those of other broods on corresponding dates. Favorable fall weather prolonging the 1951 growing season into late September beyond the time of retirement in other years may have permitted many of them to attain adult size.

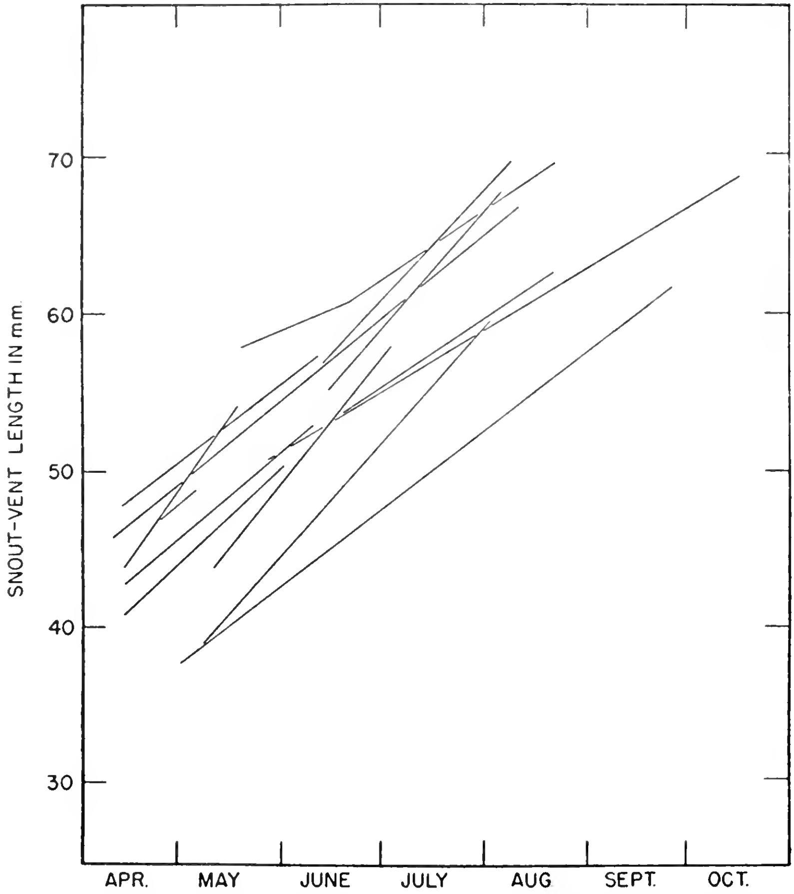

Fig. 16. Records of immature individual skinks marked and recaptured within the same growing season, showing the trend of rapid growth, and differences in growth rate between individuals.

The varying fortunes of the several annual broods studied were closely correlated with weather trends, and suggest possible effects of slight changes in climate. An unfavorable sequence of weather might bring about drastic reduction of the population without causing any direct mortality. A late spring in two successive years would have cumulative effect in delaying emergence and breeding of adults the first year, and delaying in the second year emergence of the young, already retarded by the lateness of their hatching. If this sequence were followed by onset of unusually cool and dry weather in early September, or even in late August, the young might be "caught short," and forced to hibernate while still in the 50-60 mm. size class. Emerging the following spring, they might have failed to mature sexually, reducing by perhaps half the number of productive adults. At the northern extreme of the species' range, length of growing season may be more critical than extremes of temperature in limiting the numbers and distribution. Growing seasons that average long enough and warm enough to permit attainment of maturity by onset of the second hibernation period may be essential to the species. While no two annual broods of young in the same locality come under exactly the same weather influences, extremes of retardation or acceleration continuing throughout development are relatively rare. Retarding effects of unfavorable weather causing delayed breeding and hatching, may be offset by prolongation of warm weather in the fall thus delaying hibernation, or by warm spring weather hastening emergence from hibernation.

Under favorable conditions an adult female produces about ten offspring annually of which about half are females. It is calculated that if all survived, after ten breeding seasons, the progeny of an original female might have increased to a population of more than 97,000, under the climatic conditions of eastern Kansas, permitting attainment of breeding maturity late in the second year of life. In the same ten year period under climatic conditions delaying maturity until late in the third year of life (as seems normally to occur in *E. septentrionalis* and *E. skiltonianus,* and probably in *E. fasciatus* at the northern edge of its range) the original female would have produced a population of somewhat less than 7,800 assuming that all survived. With a long growing season such as occurs in the southern part of the range, it seems theoretically possible (though not probable) that individuals might mature before the end of their first year, in time to participate in the next breeding season. If this should occur the original female might produce a population of more than 120 million by the end of the tenth breeding season.

CHANGES IN PATTERN

Progressive alteration of the color pattern is more rapid in males than in females and is synchronized with growth. During the first year of life changes in the pattern are gradual, and consist chiefly of loss in vividness. The blue of the tail is slightly dulled. The light lines become suffused with brown and the dorsolateral dark areas become paler, with light brown areas appearing on the corners of the scales and gradually spreading to replace the original black. In skinks that are in the second year of life the striped pattern although still conspicuous is made up of two shades of brown instead of the earlier black and white markings.

Even in hatchlings, the dorsal part of the rostrum and the internasals are of a somewhat neutral brownish color, matching neither the light lines nor the dark interspaces of the striped body pattern. With advancing age this neutral brown color gradually spreads posteriorly on the head so that the striking lyrate marking of the bifurcated dorsal stripe on the head in the juvenile become obscured by the time the skink has grown to small adult size, at 21 months. The top of the head is then dull brown, with a slightly mottled appearance caused by the different intensity of pigmentation in different areas. The stripes though still discernible, are faint and

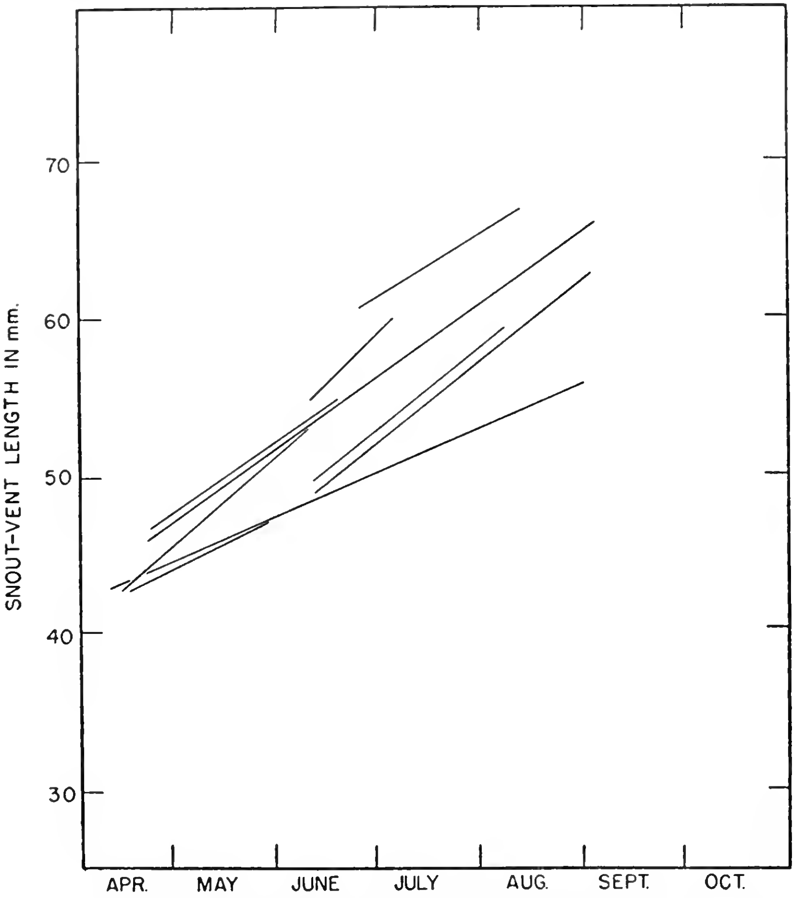

Fig. 17. Records of another group of immature skinks marked and recaptured within the same growing season.

inconspicuous. Dorsally, on the body, the stripes are still conspicuous, but are dull and lacking in contrast. At this stage, the dark lateral area is retained with intensity of pigmentation scarcely diminished.

TABLE 13. NORMAL RANGE OF VARIATION IN DORSAL STRIPING OF HEAD AND BODY, AND IN COLOR OF TAIL ACCORDING TO AGE AND SEX.

Age, Size and Sex	Condition of stripes					Color of tail	
	Sharp	Distinct	Dull	Faint	Absent	Original	Regenerated
Small young						bright blue	bright blue
body.........	X						
head..........	X						
Larger young						bright blue	duller blue
body.........	X						
head..........	X	X					
Young adult female						dull blue	gray-blue to brown
body.........	X	X					
head..........		X	X	X			
Young adult male						mostly dull blue	gray-blue to brown
body.........		X	X				
head..........			X	X	X		
3 year adult female						mostly brown and gray with scattered blue scales	mostly brown and gray
body.........			X	X			
head..........				X	X		
3 year adult male						mostly brown; occasional bluish scales	brown
body.........					X		
head..........					X		
Old adult female						brown; occasional bluish scales	brown
body.........			X	X	X		
head..........					X		
Old adult male						brown	brown
body.........					X		
head..........					X		

In tracing the gradual ontogenetic changes in the striped pattern, from the vividly contrasting colors of hatchlings to the dull, patternless coloration of old adult males, five descriptive terms have been applied to the successive stages: "sharp," "distinct," "dull," "faint," and "absent." To most individuals below minimum adult size, the term "sharp" is applicable, although there is some loss in vividness in the larger young, as compared with hatchlings. Fading of the original striped pattern proceeds more rapidly on the head than on the body. Upon emergence from their second hibernation at an age of about 21 months, the skinks, mostly grown to adult size, and ready to mature sexually, still show but little sexual difference. They retain the hatchling pattern essentially unchanged, but with colors dulled and contrasts reduced. Within a few weeks the newly matured males undergo relatively rapid color change as the breeding season progresses. The stripes tend to fade and blend into the dark areas adjacent to them. In the two-year-old males stripes are distinct to dull on the body and faint or absent on the head, while in females of the same age group, body stripes are sharp or distinct.

Table 13 refers to adult pattern and coloration as they appear in the breeding season. After the breeding season, in late spring and early summer, when the red suffusion of the head and neck has faded in adult males, the original striped pattern, after having been almost completely suppressed may again become discernible. Individuals of the same size differ in extent of pattern change, and the color descriptions made of individuals were not sufficiently detailed to show fully the changes occurring between successive dates of capture. However, most large adult males taken later than mid-June had at least some trace of the striped body pattern and many of them had become so much like females in appearance that close scrutiny was necessary to determine their sex. They were especially like females in having the dark lateral area extending forward onto the cheek and setting it off sharply from the paler temporal region above it. In breeding males the head has no such dark markings and is suffused with red.

Growth and Regeneration of the Tail

Even among those skinks which have never broken their tails there is a wide range of variation in relative length of tail. This is partly a matter of relative growth since the proportions change during the course of development. Also there may be slight sexual difference and there is much individual variation. In fetuses still well below hatching size, the tail length is less than the snout-vent length. For instance, an egg in a natural nest 12 days short of hatching contained a fetus that had a snout-vent length of 14 mm. and tail length of 12 mm. (Figure 18). In the late stages of fetal development the tail growth is relatively rapid. At hatching, the tail is considerably more than half the total length. In a large series of young with snout-vent lengths from 30 mm. down to hatching size of 25 mm. or less, the tail length averaged 130.8 per cent of snout-vent length. In larger young, up to a snout-vent length of 40 mm. or more, the tail continues to lengthen more rapidly than the body. In skinks that are about two thirds grown, the tails average relatively longer than in either larger or smaller individuals. In the sample representing the size class 50-54 mm. snout-vent length, the tails average 163.3 per cent of the snout-vent lengths, whereas in groups of adults of various sizes and both sexes, the tail length is near 155 or 156 per cent of the snout-vent length. Sexual dimorphism in tail length is slight if it exists at all; in adult males, tails averaged a little longer than in adult females.

When a skink's tail is broken, there is almost no loss of blood. The fractured surface is rough and irregular, with exposed muscle masses protruding on the detached end and corresponding concavities on the end of the stump tail retained by the lizard. The concavities are soon filled with oozing blood, and a thick scab forms. As healing begins, the broken end presents a flat, slightly irregular surface. When the scab is sloughed off, a slightly convex surface of delicate, pale-colored new skin of the regenerating tail, is exposed. At first, no scale structure is discernible. As growth proceeds, the new tail takes on a bluntly conical shape. During the early stages of growth, it is well set off from the original portion by the abrupt

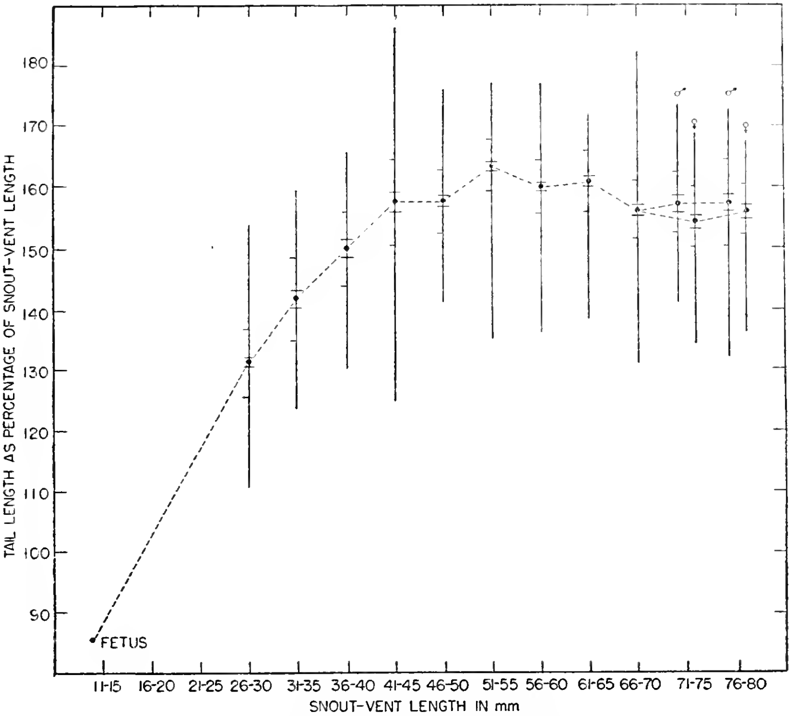

FIG. 18. Diagram showing relative tail-length (as a percentage of snout-vent length) in skinks of different size groups that retain their original tails unbroken; in the early stages of growth the tail becomes relatively longer as size increases, but the trend is reversed before adult size is attained. For each series the mean, standard error, standard deviation, and extremes are shown.

taper at the point of contact and by its paler coloration and different texture, with no scales discernible at first, and later with fine and granular scalation. The new tail elongates until the more abrupt taper beyond the point of the break is no longer noticeable, and the coloration, surface texture and scalation match that of the original portion so closely that it is difficult to determine where the break occurred or even to ascertain that there has been one. On the regenerated tail, however, the scales are less uniform in size and less regular in shape. The regenerated tail, being different from the original in internal structure, with a cartilaginous rod replacing the vertebral column, is less fragile and subsequent fractures are most likely to be on the part proximal to the regeneration. Nevertheless, fractures of regenerated tails occur occasionally. In old skinks especially, the tail eventually may consist of three or more distinct segments including the basal remnant of the original tail and the successive regenerations. When a break in the regenerated tail occurs, the detached portion is relatively inert, and is capable of only feeble twitching movements in contrast with the lively wriggling normally displayed in a newly detached tail that includes part of the central nervous system.

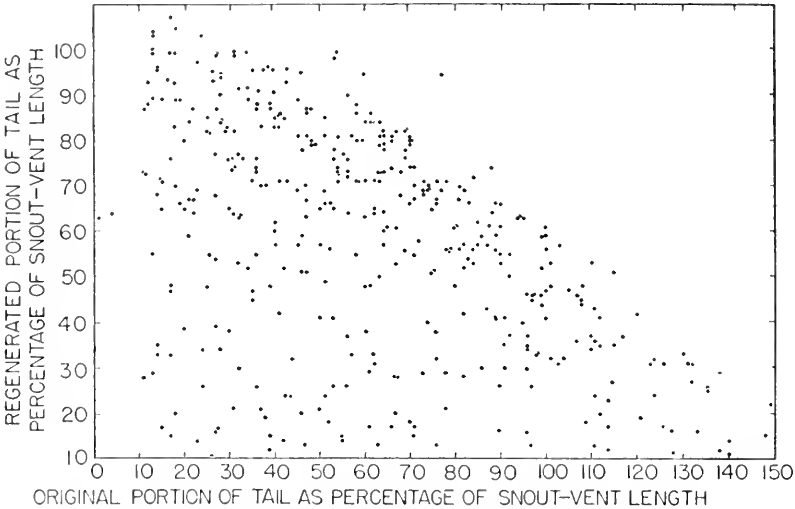

FIG. 19. Relative lengths of original and regenerated portions of tails in skinks which have had their tails broken and regenerated; for each individual, length of each part of the tail is expressed as a percentage of the snout-vent length.

Rate of growth in the regenerating tail is controlled by a variety of factors, such as age, condition, and activity of the individual, and site of the fracture. A break occurring early in the skink's lifetime results in regeneration more complete than occurs in an adult sustaining the same type of injury. The regenerated tail eventually may be longer and thicker than the lost part if the lizard is young and still growing. But the regenerated tail is never so long as the original one would have been. Regeneration is most extensive in those tails broken near the base. The farther from the base the break occurs the shorter is the part regenerated. As a result, tails that have had time to regenerate do not differ greatly in total length regardless of where the break occurred. However, the nearer the break is to the base, the shorter is the total tail-length after regeneration (Figures 19 and 20). If only the tip of the tail is lost, regeneration may not occur. In the skinks examined that had regenerated tails the proportions varied over a wide range. Presumably, in many, growth of the regenerated portion was still incomplete.

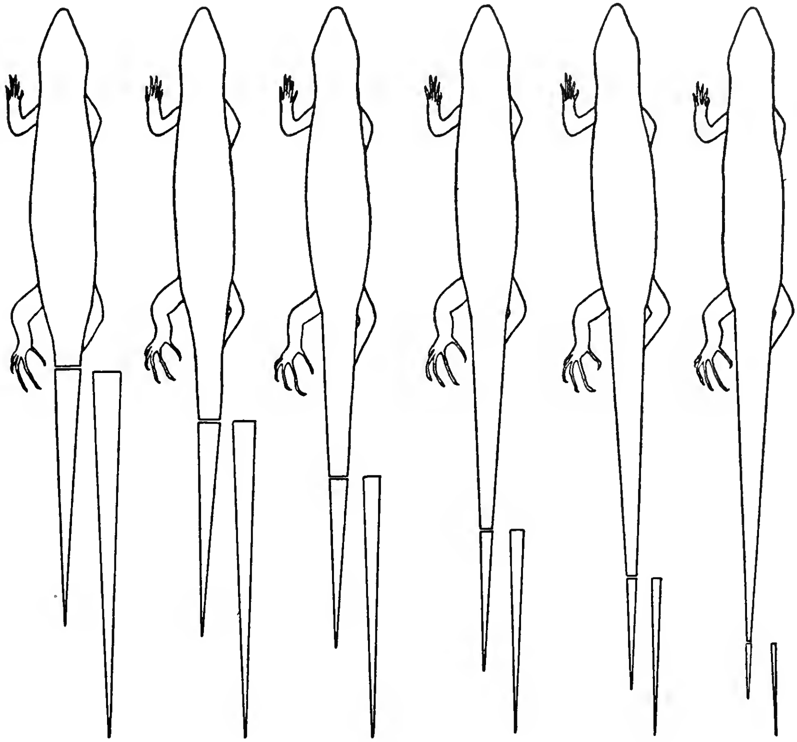

FIG. 20. Diagrams showing typical extent of tail regeneration in skinks having tails broken at different points, × approximately ⅔. Original parts of the tails are at the right.

Under favorable conditions regeneration occurs at a relatively rapid rate. After a period of healing the new tail grows with a sudden spurt, making most of its gain in length within a few weeks. Then growth abruptly slows or ceases altogether. In young similarly rapid growth of the regenerating tail occurs, but subsequently

TABLE 14. RECORDS OF REGENERATION OF THE TAIL IN INDIVIDUAL SKINKS MARKED AND RECAPTURED.

Age and Sex	Date	Snout-vent length in mm.	Tail length in mm.
No. 1. Adult male	June 1, 1951	73	38 (newly broken)
	June 26, 1951	73	38+14
	August 17, 1951	76	40+45
	April 29, 1952	76	40+45
No. 2. Immature	May 28, 1949	51	46 (newly broken)
	October 15, 1949	69	51+21
No. 3. Immature	June 11, 1950	49	49 (newly broken)
	September 2, 1950	63	63+31
No. 4. Immature female	August 10, 1950	62½	60 (newly broken)
	June 14, 1951	68	62+17
No. 5. Adult male	August 14, 1950	67½	77+4½
	September 3, 1950	68½	77+6½
	April 27, 1951	69	78+9
No. 6. Adult male	April 7, 1950	67	38 (newly broken; separated end 66)
	July 27, 1950	71	39+47½
No. 7. Adult male	May 28, 1951	70	18 (newly broken; separated end 100)
	June 14, 1951	71	18+1
	September 22, 1951	76	19+29+7½
No. 8. Adult male	June 12, 1951	72	33 (recently broken)
	July 28, 1951	76	36+31
No. 9. Juvenile	May 2, 1951	45	47+1
	May 14, 1951	45	47+3
	May 19, 1951	45	47+5
No. 10. Subadult female	June 7, 1952	64	51 (recently broken)
	June 24, 1952	64	51+11
No. 11. Juvenile	August 19, 1949	42	40 (newly broken)
	June 13, 1950	58½	58+28
	August 5, 1950	63	62+31
No. 12. Adult male	May 17, 1951	78	20 (newly broken)
	June 12, 1951	78	20+13

the increase is more gradual corresponding to the over-all growth of the lizard. In numerous adult skinks marked, and recorded as having well-regenerated tails, the proportions recorded at subsequent captures months or years later were still just the same, demonstrating that extent of regeneration is not proportional to elapsed time. Those adult skinks having unusually long regenerated tails presumably are individuals in which the original tail was lost early in life, and the potentiality for regeneration is probably somewhat less in older individuals, especially those that have stopped growing.

Successive records of selected individuals are listed in Table 14 to illustrate trends in regeneration of the tail. In those instances in which the tail is referred to as "newly broken" the separation usually occurred as an accident at the time the lizard was captured, while in those designated as "recently broken" separation had already occurred in some earlier accident but regeneration was not yet perceptibly underway. In the "Tail length" column, plus signs separate the original portion of tail, on the left, from the regenerated portion, on the right.

As in many other kinds of lizards, the tail in the five-lined skink serves as a reservoir for fat, which may be drawn upon for nutrition in time of food scarcity. An individual that is in good condition has a plump and rounded tail. Fat comprises much of its bulk. Upon emergence from hibernation this fat supply is not noticeably depleted. Brooding females in the latter part of the incubation period have the supply of caudal fat most noticeably depleted, and their tails may appear emaciated, with kinks on the terminal portion. It is my impression that in adults the capacity for storage of fat is most developed in the females, and that their tails vary in proportions more than do those of males. The capacity to shed the tail easily seems somewhat inconsistent with this function of fat storage. Loss of the tail sometimes involves loss of a large amount of reserve fat. Many detached tails that were broken accidentally at the time of the skinks' captures were weighed. In those that were broken off near the base and were not previously regenerated, weights were usually 16 to 20 percent of the lizards' total weights.

Movements

Data obtained concerning the movements of these skinks demonstrated that individuals tend to limit their activities to small areas thoroughly familiar to them, and wander but little. Although the nature and extent of movements in reptiles in general, and in lizards especially, are poorly known, my findings are perhaps what might be expected from the studies of earlier workers on various other species of reptiles.

Goin and Goin (1951:29) observed that *Eumeces laticeps* in Florida lives in hollow stumps, each individual excluding other adults from its stump but tolerating young. Movements have not been studied in detail in any member of the Scincidae, however. The observations of Goin and Goin, and those of other authors, seem to indicate that *E. laticeps* is territorial, and that each individual centers its activities about a tree or snag, regularly using the same hollow as a shelter and home base. In contrast, *E. fasciatus* is not territorial and has no regular home base.

The iguanid genus *Sceloporus* is perhaps better known than any other kind of lizard as regards its movements. Studies by Newman and Patterson (1909), Stebbins and Robinson (1946), and Fitch (1940) on three different species have shown that individuals of *Sceloporus* keep to small individual areas, and that territoriality is well developed, in some species at least.

Among other reptiles, turtles are much better known, as detailed studies of movements have been made on several species, of which the life histories and ecology have been thoroughly investigated (Nichols, 1939; Cagle, 1942 and 1944; Woodbury and Hardy, 1948; Stickel, 1950). They have been found to have well-defined and fairly extensive home ranges, which are not defended as territories. Studies of movements in several different kinds of snakes, by Blanchard and Finster (1933), Stickel and Cope (1947), Fitch (1949), Lowe and Norris (1950), and Carpenter (1952) have shown that these reptiles usually have definite home ranges, which may be several or many acres in extent. Their home ranges are not defended as territories against other members of the species. In general, turtles and snakes have been found to occupy home ranges that are much larger than those of lizards.

Most information concerning movements of *Eumeces fasciatus* has been obtained from the recapture of marked individuals. Actual distances of travel, and the time, frequency and motivation of movement was uncertain. A skink marked, recorded, and subsequently recaptured at a second location may have wandered widely in the meantime, visiting points relatively remote from either location of capture. The two points of capture may be within a home range regularly or occasionally covered by the individual in the course of its routine activities; or the second point may have been recorded only after a permanent shift of activities away from the area within which the original point was located. Various types of movements probably were involved.

Interpretation of the records is difficult because of the paucity of direct observations on the behavior and movements of skinks under natural conditions. Often when one is alarmed, it will run as much as 30 feet, in a fairly direct course, to a tree or bush or rock where it can find refuge. Undisturbed individuals move about slowly and circuitously. It is difficult to keep one under observation for any length of time because of the secretive habits causing it to keep under cover, as much as possible while moving about, and to hide in response to any slight disturbance.

It is obvious that individuals shift their activities from time to time, occupying new areas either abruptly or by gradual stages. Even though a successful skink has a life span of several or many years, the populations on the small study areas were found to be much altered from one year to the next. Presumably this change was brought about largely by shifts in home ranges. Several shifts of hundreds of feet were recorded, but the chances of recovering marked individuals that moved so far were relatively poor because their movements generally took them beyond the limits of the study area to locations where recapture was unlikely. Skinks often were caught at their hiding places beneath rocks or other sheltering objects. In many of these instances it was evident from the position, temperature and state of activity of the lizard that it had been in the open but had become alarmed as the collector drew near and had retreated unnoticed to its shelter just before capture, whereas in other instances it was obviously at rest in its chosen shelter. Except for females in their nest burrows individuals were not ordinarily recaptured regularly at the same hiding places. They may seek new hiding places after each period of activity.

However many of the skinks captured were taken again, after long intervals, near the same places. Time elapsed between successive captures for different individuals ranged from one day to 47 months. Of the total of 323 recaptured by September, 1952, approximately half, 162, were taken after intervals including one or more hibernation periods. In appraising home ranges and detecting the occasional shifts over a relatively long time span, chronology of the records needs to be taken into account. Records clustering about the same center seem to indicate continued occupancy of an established home range. However, when one or more early records are well separated from one or more later records, a shift in range seems probable. In some instances successive records were progressively farther from the starting point suggesting two or more shifts in the same direction from an original home range.

Although recorded movements varied from a few inches to hundreds of yards, the most noteworthy feature in general was the short distance between points of capture (considered in relation to the potential mobility of the lizards) after days, weeks, months or years. In many instances no movement was demonstrable, even though successive points of capture were not exactly the same. Named natural landmarks, mostly trees, boulders and logs, well distributed over the study area, were used as a basis for locating points on the map. Direction and distance in feet to the nearest landmark was recorded for each site of capture, but for distances of more than 25 feet estimates were made to the nearest ten feet. Usually at least one landmark was available within a 50-foot radius from any point where a capture was made. Occasional estimates made for distances of more than 50 feet, or even more than 100 feet, in the absence of suitable landmarks nearby, were sources of inaccuracy. For such estimates errors of up to ten feet were common, and some errors of greater magnitude were made.

For most individuals successive sites of capture tended to cluster within a small area, but the occasional outlying capture sites indicate that each individual does range outside the area in which its activities are concentrated. These occasional excursions cannot be consistently attributed to any one ecologic requirement, nor are they limited to any particular time within the season of activity. Adult males, however, tend to make longer movements in the brief period of concentrated sexual activity, thereby increasing their chances of finding mates. Similarly, adult females may wander beyond their usual ranges in search of suitable nesting sites. The home range may be thought of as consisting of a small central portion where activities are largely concentrated, and an outer area several times as large, familiar to the animal but used to a lesser extent by it. The activities gradually become more diffuse farther from the central part of the home range. In the five-lined skink, home ranges are unlikely to approximate the circular shape because they are molded with respect to environmental features that are not uniformly distributed. A rotting log, an old tree with decayed hollow base and nearby fallen slabs of bark and dead limbs, a rock outcrop with numerous deep holes and crevices, or a group of flat rocks in a forest glade fulfill requirements not met in the surrounding habitat with the result that home ranges are built around them.

Consequently a home range may be long and narrow, with maximum diameter several times the minimum diameter.

The usual concept of home range, as a finite area with well defined boundaries is not entirely satisfactory for an animal with the habits of the five-lined skink. The skink spends much of its time in inactivity underground or otherwise concealed and sheltered, and when it does move about it takes advantage of natural travelways over rock surfaces, tree trunks, and logs. If a log happens to be the home range center, the skink may travel the length of the log many times without making a comparable trip at right angles to this axis of travel, although it may make short side dashes to secure food. On more extended forays, the directional sequence of movements is largely controlled by the distribution of suitable cover and travel routes, as the skink avoids both open areas and dense vegetation. Outlying portions of the home range probably are not uniformly covered but are reached only occasionally as the lizard is led along some natural travel route, or after it has visited, in succession, a series of locations attractive in providing shelter or food.

Marked skinks were recaptured at distances up to 680 feet from points of original capture. Considering only the most remote points of capture for those individuals recaptured more than once, the average recorded movement for the entire group of 323 recaptured skinks was 58 feet. This figure provides a basis for comparing vagility of this species with others. Eliminating some individuals of indefinite status, the average movement for 75 adult males was 69 feet; for 102 adult females, 45 feet; and for 112 young, 61 feet. For the adult females, home range data are biased by the fact that many were caught repeatedly at or near their nests. It is not clear whether females that do not have nests range less widely than males.

Only 15 individuals, less than five per cent, had moved more than 250 feet. These longest movements were: 680 feet, adult female, 26 months; 680 feet, adult female, 10 months; 680 feet, subadult male, one year; 650 feet, young to adult male, 22 months; 640 feet, subadult to adult female, two years; 535 feet, young male, 11 months; 510 feet, adult male, 11 months; 490 feet, young (sex undetermined), 10 months; 450 feet, young male, 13 months; 350 feet, young (sex undetermined), 10½ months; 335 feet, adult female 13½ months; 275 feet, adult male, 35 months; 275 feet, adult male, 24 months; 270 feet, young to adult male, 12½ months.

For those skinks caught on only two occasions, at different places, the single movement record provides some clue as to the location and size of the home range. No evidence was obtained to indicate that the activities of these lizards center at fixed home bases. It may be assumed that any two successive captures of the same individual separated by a substantial time interval, will be distributed at random to each other within the area to which the animal's activities are confined. The varied techniques of capture, by hand and with different types of traps, would help to secure random distribution of capture sites. If the home range were covered uniformly by the animal in the course of its activities, any two random capture sites would be on the average separated by a distance equal to half the home range diameter. If the animal tends to concentrate its activities in the central part of the home range, as seems to be the case, the capture sites will be correspondingly closer together. For the 196 skinks that were caught on only two occasions, average movement was 62 feet. Within this group the 42 adult males that were recaptured only once had averaged movements of 58 feet. One had made an exceptionally long movement of 510 feet, which obviously was not entirely within its home range. Excluding this one long movement, the remaining 41 had moved on the average, approximately 47 feet (Table 15). Among the other skinks caught only twice one of 61 females and 8 of 93 young had likewise made such long shifts that it seemed inadvisable to include them in computing the size of the home range.

Distance between points of capture showed little correlation with elapsed time. For 24 of the adult males that were recaptured in the same year they were originally marked, the average distance was 49 feet, whereas in the 17 others recaptured after one or more hibernations the average movement was 45 feet. For adult females, the corresponding figures were, respectively, 22 feet and 29 feet; and for young, 33 feet and 66 feet.

For those individuals recaptured twice, at different locations, the three points of capture show to a greater or lesser degree the position, and, in part, the extent of the home range. Of course, all three points may be concentrated near the center of the home range, or they all may be scattered along its edges. In general, however, each point will lie somewhere between the center and edge of the home range, separated from each of the other two points by a distance of, on the average, approximately a home range radius.

Table 15 shows that adult males and young tend to range more widely than adult females, and that young tend to shift to new areas more frequently than do adults. Many of the recorded movements (in addition to the long ones that were excluded from the home range computations) may have involved short shifts in ranges. If all such shifts could be definitely identified and eliminated from the computations, actual home ranges might be considerably smaller than those indicated by the present set of data. Home ranges approximately 90 feet across for adult males and young, and a little more than 30 feet across for females are indicated. Actual area of a home range would amount to only a fraction of an acre—from about one-seventh to less than one-fiftieth. The dash of an alarmed skink to a place of refuge, though involving at most only a few seconds, may traverse a large part of its home range. Through long association the lizard is thoroughly familiar with the terrain, so that it can take full advantage of the peculiar features in escaping, hunting, traveling or resting.

TABLE 15. DISTANCES BETWEEN SUCCESSIVE SITES OF CAPTURE FOR MARKED FIVE-LINED SKINKS ON STUDY AREAS, INDICATING HOME RANGE SIZES.

Age, Sex and Number of Captures	Average maximum distance in feet between points of capture, and extremes	Number of skinks included in sample	Number of skinks discarded from sample because of relatively long movements, indicative of shifts of range
Adult males			
Individuals captured just twice	47 (225-0)	41	1
Individuals captured just three times	47 (130-0)	18	0
Individuals captured four or more times	91 (200-0)	17	2
Adult females			
Individuals captured just twice	16 (90-0)	56	4
Individuals captured just three times	25 (90-0)	25	3
Individuals captured four or more times	28 (90-0)	15	1
Young			
Individuals captured just twice	45 (160-0)	85	8
Individuals captured just three times	46 (150-0)	14	0
Individuals captured four or more times	82 (175-0)	14	2

Relatively few marked individuals were caught four or more times at different sites. For these individuals listed below the distribution of the sites is more or less indicative of shape and size of the home range in some instances. For some of them successive locations of capture are shown and possible home ranges are outlined in Figures 21-25.

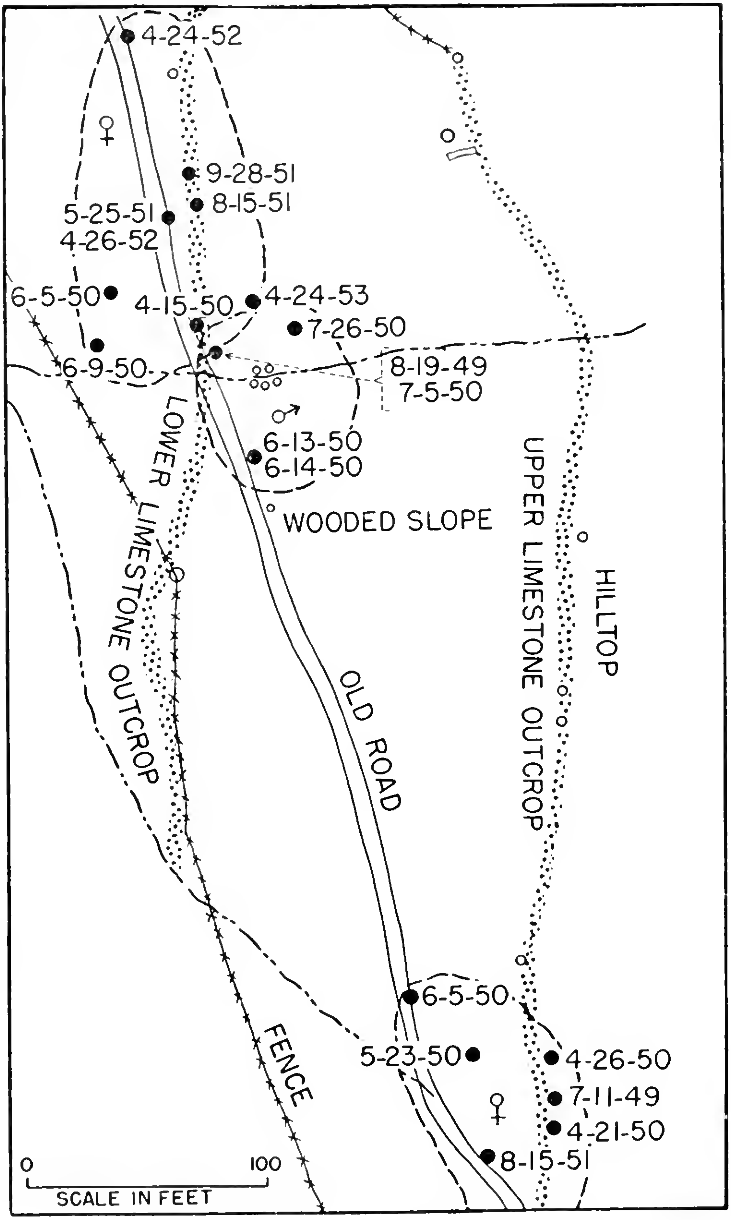

FIG. 21. Map of Skink Woods study-area, showing chief physiographic features and landmarks, and showing also successive sites and dates of capture of a marked male skink and two marked females, suggesting extent of home ranges.

ADULT MALES

No. 1: Seven captures in two years, on May 13, 1950, May 12, 1951, and in 1952 on April 28, May 1, 2, 4 and 6, these seven locations well distributed over a stretch of rocky slope 275 feet in greatest diameter. The fifth location was only 20 feet from the original, whereas the last, only four days later, was the most remote, suggesting that the whole area covered may have been within a home range.

No. 2: Seven captures in 46 months, skink not fully grown when first captured on June 22, 1949; 275 feet south on May 4, 1950; had moved from this second location 150 feet west northwest on June 17, 1950, and this third location together with the last four, on May 15, 1951, and May 13 and 15, 1952, and April 6, 1953, were all within a 20 foot diameter. Evidently two shifts in range were involved.

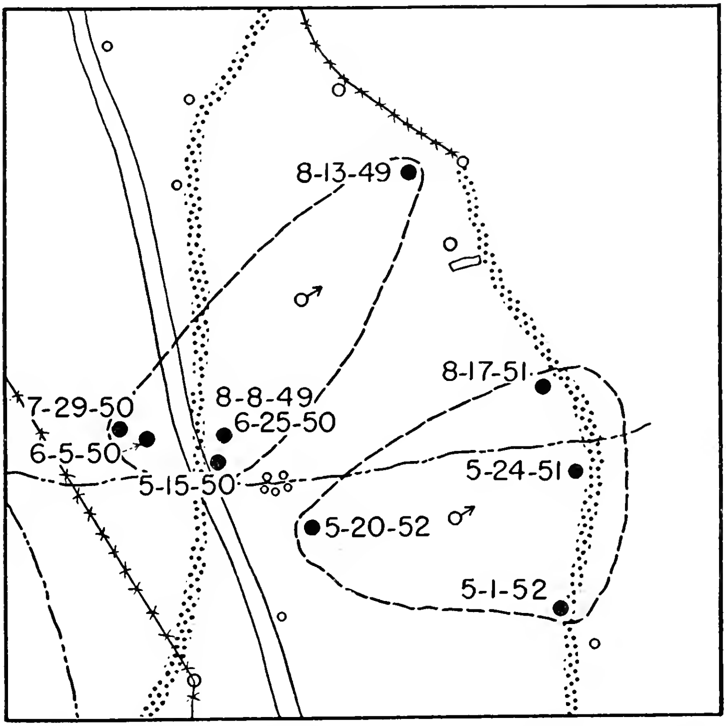

FIG. 22. Sites of successive captures of two marked adult males in the Skink Woods study-area.

No. 3: Six captures, all at different locations, in 22 months, on July 5 and 28, 1950, May 3 and 23, and June 21, 1951, and May 1, 1952. The 190-foot-wide area was probably all within a home range, as the fourth and fifth sites were those most remote from each other.

No. 4: Six captures in 21 months, in 1950 on August 14 and September 3, in 1951 on April 27 and August 21, and in 1952, on May 28 and 30. The four 1950 and 1951 locations were within a 30-foot diameter, whereas the two 1952 locations were 150 feet farther east, and even nearer together, suggesting a shift in range.

No. 5: Five captures in five months, all within a 40-foot diameter, on April 24, May 7 and 28, June 14, and September 22, 1951. The first and third locations were at almost the same spot.

No. 6: Five captures all at different locations, in 23 months; in 1950 on July 27, in 1951 on April 30 and May 25, and in 1952, on May 1 and June 28. The second, third and fourth locations were all within 45 feet of each other and of the first, but the last was 110 feet from the first, possibly representing a shift.

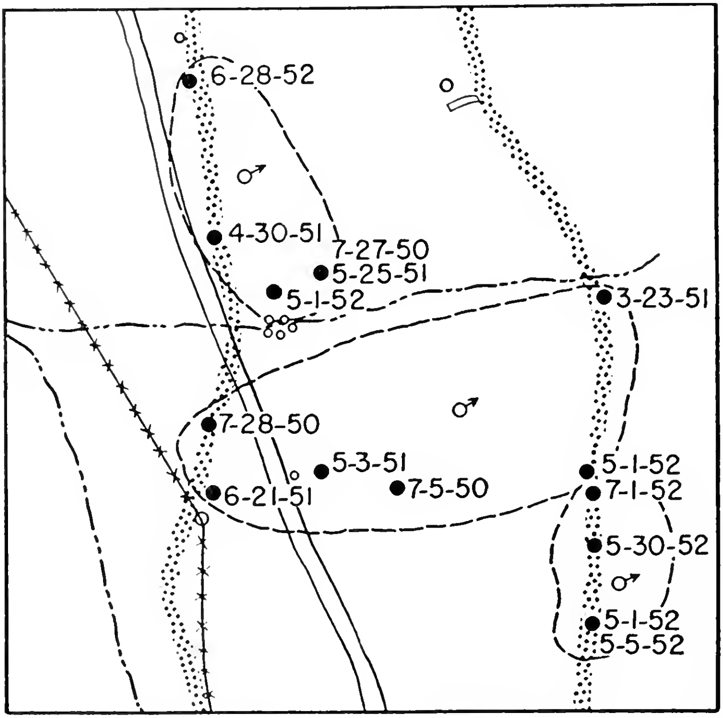

FIG. 23. Sites of successive captures of three marked adult males in the Skink Woods study-area.

No. 7: Four captures in two months, at approximately the same place on May 1 and 5, 1950; on May 30 had moved 35 feet farther north along ledge, and on July 1, 25 feet farther in the same direction.

No. 8: Four captures in one year, all at approximately the same place along rock ledge, on June 17, 1949, and April 21, May 3 and June 15, 1950; trapped three times and once caught by hand.

No. 9: Four captures in one year, on April 7 and 11, and July 27, 1950, and April 14, 1951, the four different locations all within a 30-foot diameter.

No. 10: Four captures in 22 months, in 1950 on July 7, and again on July 23, 175 feet farther north; on May 25, 1951, 200 feet east of second location, and on May 2, 1952, 30 feet from third location. At least one shift in range probably occurred, from 1950 to 1951.

No. 11: Four captures in 36 days, in 1951 on April 30, May 8 and 15, and June 5. The last two captures were made in the same trap and were only 15 feet from the original location, but the second location was 130 feet from both. Because the time span was short and the lizard returned from the most remote point, it seems probable that all four records were within its home range.

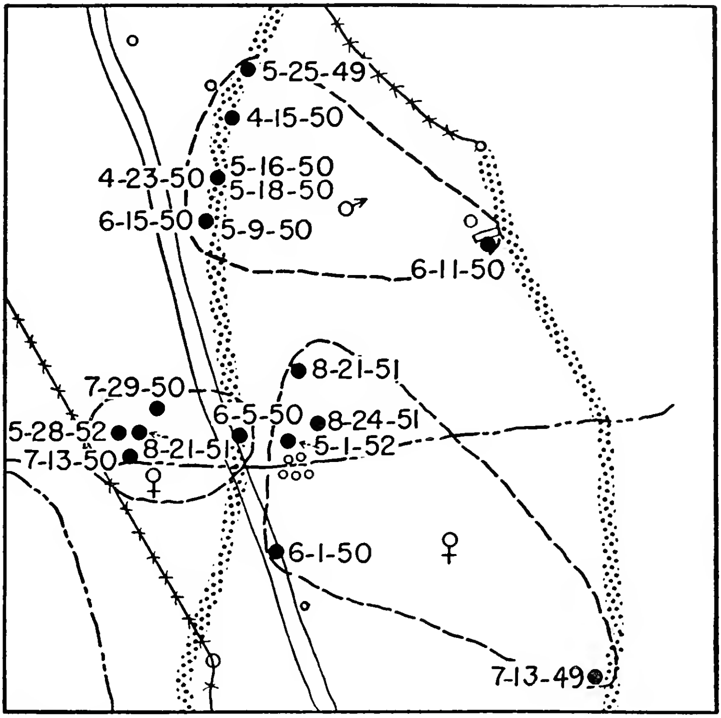

FIG. 24. Sites of successive captures of marked skinks, a male and two females, in the Skink Woods study-area.

No. 12: Four captures in 11 months, all within a 50-foot diameter, in 1951, on June 1 and 26, and August 27, and in 1952, on April 29.

No. 13: Four captures in 15 days, all in July 1949 within a 10-foot diameter.

No. 14: Four captures in 22 months, July 22, 1950 (as subadult), in 1951, on May 8 and June 5, and on May 13, 1952. Second location 295 feet southwest of first, third 30 feet north of second, and fourth 650 feet east of second and third. Probably two shifts of range were involved.

ADULT FEMALES

No. 1: Six captures in 26 months; in 1950 at the same place on June 4 and 13, in 1951 on May 26 it had moved from the original quarry ledge location 680 feet south southeast down the slope to the pond rock pile, where recaptured on June 9, and in 1952 on May 21 and July 22.

No. 2: Six captures at four locations all within a 25-foot diameter, in 13 months; June 5, 1950, and May 25, June 18, 26 and 29, 1952. On each occasion this female was hiding in a nest burrow, but she shifted to new nest sites as a result of disturbance by the investigator or flooding when there were unusually heavy rains.

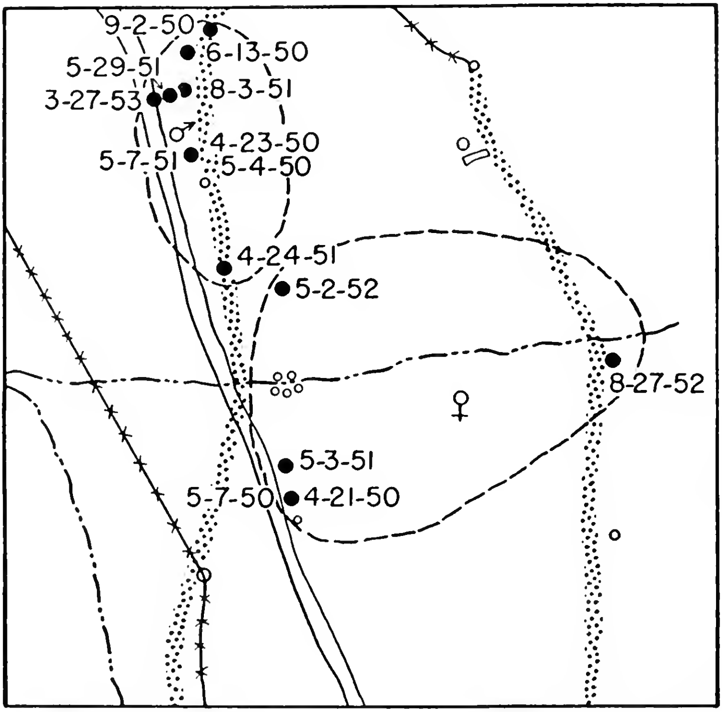

FIG. 25. Sites of successive captures of a marked male and a marked female, each taken in three different years in the Skink Woods study-area.

No. 3: Five captures in 34 months, all within a radius of a few yards, at the pond rock pile, on August 8, 1949, June 5 and July 23, 1951, and May 15 and June 4, 1952.

No. 4: Four captures in 34 months, all within a radius of a few yards at the pond rock pile, on August 8, 1949, June 7, 1950, May 30, 1951 and May 21,

1952. It is notable that this female was taken only once in each of four different years, her occupancy of this rock pile seemingly continuing throughout the duration of the study.

No. 5: Four captures in two months, in 1950 on April 15, and on April 26 had moved 50 feet south; on May 23 she was approximately 50 feet from both second and third locations, and on June 5 was between second and third locations.

No. 6: Four captures in 23 months, all within a 20-foot stretch of ledge, in 1950 on June 5 and 17, in 1951 on August 22, and in 1952 on May 1.

No. 7: Four captures in one year, in 1951 on May 19, June 12, June 24, and in 1952 on May 21, all four locations within a 15-foot diameter.

No. 8: Four captures in 23 months, in 1950 on July 5 (as a subadult), in 1951 on August 6 and 15, and in 1952 on May 28, all within a radius of a few yards at the pond rock pile.

No. 9: Four captures in 13 months, on August 2 and 3, 1951, and May 28 and August 31, 1952. From the original location successive sites were 30 feet southwest, 20 feet south southwest, and 30 feet north.

YOUNG

No. 1: (male) Five captures in 33½ months; marked as hatchling on July 13, 1949, and recaptured on June 1, 1950, 175 feet northwest down slope. Subsequent locations of this lizard, as an adult, were, in 1951, on August 21 and 24, and 1952 on May 1, 80 feet east, 80 feet east, and 70 feet northeast from the second location.

No. 2: (male) Five captures in a little more than one year, all within a radius of a few yards at the pond rock pile, in 1949 on August 23, and in 1950 on June 7, July 23, August 19, and September 3.

No. 4: (male) Four captures in 11 months all within a 30-foot stretch along the ledge, in 1950 on July 4, and in 1951 on May 6, 14, and 25.

No. 5: (male) Four captures in one year, in 1950 on September 4, and in 1951 on May 11, June 14, and August 21; the first and last locations were together separated from the second and third, also together, by about 20 feet.

No. 6: (male) Four captures in 13 months, in 1950 on April 19, June 5 and June 6, and in 1951 on May 14. All four locations were linearly distributed along the ledge, the second and third near together 30 feet north of the first and the fourth 30 feet south of the first.

No. 7: (sex undetermined) Four captures in one month, on April 24, and May 2, 4, and 21, 1952, well scattered within a 70-foot diameter.

No. 8: (female) Eight captures in 25 months, in 1950 on June 5 and 9, and in 1951 on May 25, August 15, and September 28, and in 1952 on April 24 and 26. All were within a 150-foot diameter, the first three all within 40 feet, the fifth and sixth near together but 35 feet north northeast from the first group, the last three all within a 90-foot diameter and all to the north of the first five. At least one shift probably was involved.

No. 9: (female) Five captures in 28 months, in 1950 on April 21 and May 7, in 1951 on May 3, and in 1952 on May 2 and August 27. The first three captures were all at approximately the same location, from which the fourth was 60 feet north and the fifth was 130 feet east.

No. 10: (female) Five captures in 24 months; in 1950 on June 5 and 13, and July 29, in 1951 on August 21, and in 1952 on May 28. From the original location successive captures were 50 feet west, 35 feet west northwest, 40 feet west, and 50 feet west.

Less complete records of the movements of other individuals are included along with growth data, on pages 79 to 82 and 87 to 88.

Sizes of home ranges are affected by the type of habitat. For instance, the pond rock pile approximately 70 x 30 feet, must have constituted the entire home range for the many individuals living in it, since it was surrounded by areas that did not provide suitable habitat. No less than 212 five-lined skinks were taken in this small rock pile area in four seasons, and it is obvious that many of these were occupying it simultaneously since a substantial proportion of the total were caught there in more than one year. This rock pile provided in particularly concentrated form the essential habitat requirements, such as an abundant and varied arthropod food supply, an almost infinitely large number of hiding places beneath and between the rocks, basking sites, and flat rocks with damp soil beneath, suitable for nests. In open woods home ranges tend to be larger or, at least, more elongate. Scattered distribution of such habitat features as flat rocks and outcrops, stumps, logs, and glades with patches of sunlight, may induce an individual to extend its activities over a more extensive area. For some of the adult males for which largest numbers of records are available, showing repeated movements back and forth within a definite area which seemingly constituted a home range, movements of 275 feet, 225 feet, 170 feet, 165 feet, 150 feet and 130 feet, respectively, have been recorded. For one young which grew to the size of a subadult during the period covered by the records, movements within a 150-foot diameter were recorded. These individuals all had home ranges substantially larger than the average. It seems that in the five-lined skink there is no fixed size or shape for a home range, but that it varies within rather wide limits depending on age, sex, and perhaps individual peculiarities and on the presence and distribution of essential habitat features within the general area.

Most of the young that were recaptured had grown to subadult or adult size, so that the movements they made as young cannot be separated from those made when they were full grown or nearly so. For 40, however, recapture records are available while they were still less than 56 mm. long. One of those was an exceptionally long movement of 215 feet, obviously involving a shift of range. For the other 39, the average movement was 34 feet, almost intermediate between the average movements of adult males and females. Observations on recently hatched young have given the impression that they keep to narrowly limited areas probably only a few yards in extent at first. For instance, at various times several members of a brood of young have been observed foraging simultaneously but independently on the same 10-foot log, within a few feet of each other. For periods of up to more than a week they had failed to disperse any farther than this from the nest, although probably never returning to the nest itself after having left. In subsequent weeks, however, the young are likely to shift their activities from the immediate vicinity of the nest site to more favorable near-by areas, and gradually extend their ranges. By the time they are one-fourth grown they are ranging over areas larger than those used by adult females.

Some of the shifts in range are probably forced upon individual skinks by changes in seasonal distribution of food, shelter and other requirements, causing them to abandon certain areas and invade others by gradual stages, without venturing far, at any time, into unfamiliar surroundings. Occasional individuals apparently get lost and undergo a period of wandering before they re-establish a home range. An individual venturing slightly beyond the border of its home range might lose its orientation and fail to return, especially if it left under conditions of stress, as when pursued by an enemy, or a rival of its own species. Several individuals originally captured in the vicinity of the quarry or nearby ledges, were subsequently recaptured at the pond rock pile more than 200 yards away. In these instances it may be that the lizard wandered from its home range along the ledge, and finding itself in thick woods, with nearly continuous canopy permitting insufficient sunlight, and with few rocks for shelter, it continued down the slope to the lower edge of the woods, crossed a ditch, and a 100-foot stretch of grassland, and finally reached the exceptionally favorable habitat provided by the rock pile.

The extent to which memory persists through the season of dormancy is little known, but great change takes place in the habitat during the colder half of the year when the lizard's activity is suspended. Even if the area is one that is free from gross disturbance by man or large animals, the changes occurring are so great that the area might be scarcely recognizable from the lizard's viewpoint. Herbaceous vegetation mantling the soil, at the height of its development in late summer, will have died, dried out and the leaves and stalks will have been matted down by wind, rain, and snow, and incorporated in the surface layer of soil by the next spring. Shrubs and trees having shed their leaves, present contours quite different from those in autumn. Holes and crevices familiar as avenues of escape, will have been sealed, by the weather collecting and compacting surface debris. Less extensive changes are involved in the occasional blowing down of trees and dead snags, erosion of gullies, deposition of sediment and drift wood, and disintegration of logs. Many of the invertebrates which are the main food sources in late summer, are unavailable in early spring, being at different stages in the life cycle or annual cycle of abundance; and those kinds which make up the bulk of the spring diet likewise are often unavailable in fall. These changes in location of food supply, shelter, and other needs, and the seasonal change in microhabitat, breaking the established routine of conditioned responses to habitat features would seem to promote shifts in range after emergence from hibernation. The available records tend to bear out this supposition. Of the 15 skinks recorded as making long movements of more than 250 feet that almost certainly involved shift in range, only one was recaptured the same season; the other fourteen had passed one or more hibernations.

In the course of the study approximately 30 individuals were released or accidentally escaped at places other than the locations where they were originally taken. Some of these were young hatched in the laboratory, some were of unknown origin, their locality tags having been lost before release while they were being handled in the laboratory, or escaped from defective cloth bags while they were awaiting processing or release, and some taken on remote parts of the Reservation or near-by land were deliberately released on one of the study areas with the idea that they would replace skinks of the same sex and age, recently eliminated through an accident of trapping or handling. Ten were released in Skink Woods, ten at the pond rock pile, eight at the laboratory building, and two near Rat Ledge. In no instance was a transferred skink known to have found its way back to an original home range, although some might have done so with fairly short trips of only a few hundred feet, and the chances of recapturing them would have been good. Therefore it seems that homing instinct is either wholly lacking or but feebly developed. The incidence of recaptures was low, only four for the entire group, suggesting a tendency to wander away from the area of release before settling down on a home range. One young found on May 11, 1950, in the laboratory where it probably had escaped, was released in Skink Woods, and was recaptured three times in the summer of 1951, in what seemed to be a home range within 80 feet of the point of release. Another young of unknown origin released in Skink Woods on May 18, 1950, was recaptured six days later 160 feet away. Five hatchlings from a clutch of eggs incubated and hatched in the laboratory, were released in Skink Woods on August 8, 1952. The following April two of them were recaptured, only 20 feet and 25 feet respectively, from the point of release. The movements and dispersal of this group from the point of release probably paralleled that of a typical brood dispersing from its nest after hatching under natural conditions. An adult male captured just off the Reservation was released at the pond rock pile on May 15, 1952, and was recaptured there on June 2 and June 4. In general, skinks transferred from their original location seem soon to settle down in a new range if the habitat is favorable, but establishment of a home range may or may not be preceded by an initial period of wandering.

Food Habits

McCauley (1939: 151) examined contents of 25 alimentary tracts of *E. fasciatus* collected in Maryland as the basis for the most extensive account of the food habits yet published. One tract contained a broken *Eumeces* tail, possibly that of the lizard that ate it, which had a recently broken stump tail. A half-grown skink contained numerous *Eumeces* scales, and McCauley interpreted this as indicating that it had fed on another of its own species or of *E. laticeps*. As no other hard parts of the assumed victim were in evidence, these scales may have been the lizard's own slough. (In the present study it was found that eating of the slough was far more frequent than cannibalism.) Arthropod prey included: 11 orthopterans (4 undetermined, 3 unspecified grasshoppers, 2 gryllids, 1 blattid, 1 acridid); 10 coleopterans (7 undetermined, 1 each of rhynchophoran, cerambycid, carabid, staphylinid larva, elaterid adult and larva); 8 spiders; 5 pulmonate snails; 5 flies; 3 undetermined; and one each of lepidopteran larva and adult, ant, dragonfly, thysanuran, and sow bug.

In Ohio, Conant (1940: 31) noted food items consisting largely of grasshopper nymphs and small beetles. He found that in captivity these skinks would eat mealworms, crickets, grasshoppers, spiders, roaches, and newborn mice, and a few individuals would lap egg from a mixture of chopped meat and eggs. One large male killed and ate a small common swift (*Sceloporus undulatus*). Netting (1939: 162) mentioned newborn mice, birds' eggs and small lizards as possible prey, although stating that this species is mainly insectivorous.

Taylor (1936: 61) describing the feeding habits of lizards of this genus wrote: "The food consists of a very extensive variety of insects and insect larvae, Arachnida and occasionally small crustaceans. In a few specimens traces of plant material have been observed, but I regard this as being most probably of accidental introduction in the diet. Probably the most surprising fact about the diet of the forms examined is that ants are absent." In the present study of *E. fasciatus,* the trends in general bore out Taylor's findings concerning absence of ants from the diet, although three ants were found among more than 600 other food items. These three, one of them a larva, were of the two largest species among the many kinds of ants found in the area of the study. Most of these local kinds of ants are below the minimum size of prey ordinarily taken by the skinks. Colonies of small ants, *Aphenogaster* sp., for instance, are abundant in the soil beneath flat rocks in the same situations where the skinks are found, and constitute most of the food of the small toads, *Microhyla olivacea,* which were abundant in the same habitat and microhabitat as the skinks, especially in the Skink Woods study area (Freiburg, 1951: 383).

Burt (1928: 56) without citing specific records, stated that "The food of *E. fasciatus* consists largely of insects and spiders," but in another paper (1928: 62) he listed contents of two stomachs, including a wood roach (*Parcoblatta*), a cricket (*Gryllus pennsylvanicus*), a grasshopper, and 2 spiders (attid and lycosid). Smith, summarizing the findings of other authors (1946: 350), stated that "The food consists of various small insects, insect larvae, earthworms, spiders, etc. Small vertebrates such as young lizards and mice are sometimes eaten." In a later work Smith (1950: 188) altered this statement slightly: "The food consists of almost any small moving animal, including many kinds of arthropods and even small vertebrates."

Many authors have mentioned predation on mammals by these skinks, but without citing specific instances, which must be rare indeed, for the smallest newborn mice seem to be near the maximum size of objects that could possibly be swallowed by the largest adults of the common five-lined skink. Various early records and statements pertaining to predation on small vertebrates by five-lined skinks probably pertain in most cases to *E. laticeps,* which is much larger than *E. fasciatus,* and more powerful.

Barbour (1950: 102) recorded stomach contents of an *E. fasciatus* collected in Harlan County, Kentucky, as consisting of 60 per cent Arachnida, 30 per cent adult Lepidoptera, and 10 per cent ants, by volume. Werler and McCallion (1951: 250) mentioned that on two occasions these skinks in Virginia were seen to eat tenebrionid beetles and larvae.

Webb (1949: 294) fed captive skinks with field crickets (*Gryllus*) and noted that the lizards tended to seize them by the pronotum, and then worked forward to the head, chewing vigorously to disable them. The seized crickets attempted to defend themselves by striking the lizards' faces and eyes with the cerci and tibial spines. Webb also offered his skinks newly hatched snails, *Helix aspersa,* which were noticed and fed upon when they moved. In one instance, he noted that a skink found a quiescent snail, and swallowed it after testing it with the tongue a few times.

McIlhenny (1937: 232) has published a remarkable account of observations on the foraging behavior of a large adult male skink (stated to be *E. fasciatus* but almost certainly *E. laticeps*) in southern Louisiana, which climbed among vines on the side of a house and attacked nests of wasps, *Polistes pallipes* and *P. bellicosus,* shaking out the larvae, pausing to crush and swallow the few adults that lit on it and attempted, unsuccessfully, to sting. After many larvae had been shaken to the ground the skink descended and made a leisurely search, eating them in seemingly prodigious quantities. Several times it climbed back into the vines to shake out more larvae, and each time retrieved from the ground those it could find. After feeding to repletion it returned to its habitual shelter in a hollow live oak fifty feet from the house. In a two-week period, however, it returned frequently to raid the wasp nests in the vines, and eventually it had attacked all of the 32 nests that were originally present, completely destroying many of them.

In the course of the present study direct observations on the food habits of skinks rarely could be made in the field. Most of those seen had been alarmed by the presence of the observer, and already had begun a dash for shelter. Others not sufficiently alarmed to take cover, were affected by an observer's presence, so that usually they ceased their normal activities and crouched attempting to conceal themselves or slithered nervously from one vantage point to another, on the alert for any sign of danger.

On September 1, 1951, a young skink (30-35 mm. snout-vent length) was discovered on the cement walk just outside the laboratory building, holding a cricket (*Nemobius*) which evidently it had just caught. When I came out of the building, the skink, alarmed, ran about ten feet, holding the cricket by one leg. The cricket was still alive but was nearly immobilized, except for twitching of its antennae and mandibles, and evidently it had already been shaken and battered. After maneuvering about the cement walk the skink ran through the open door into the building. Though seeming to be uneasy at my proximity it was still mainly intent on subduing and swallowing its prey. Following, I caused the skink to take alarm. It dashed back through the door to the walk outside and still carrying the cricket, it ran along the walk to the steps leading up to another building and climbed onto the first step where its uneasiness soon subsided. The cricket was remarkably large in proportion to the skink itself, being of approximately the same diameter, with a length nearly half that of the skink's snout-vent length. Nevertheless, in about five minutes the skink had swallowed it entire. As swallowing began, on the cement step, the skink was in bright sunshine of early afternoon. In less than a minute it seemed to become overheated, and dragged the prey back several inches into shadow. While swallowing was still in progress, it again ran forward till its anterior half was in sunshine, seemingly regulating its body temperature by these frequent shifts.

A similar encounter between a larger juvenile and a cricket (*Ceuthophilus*) was observed on May 9, 1953. After I had stood for several minutes beside a rock ledge in woods, my attention was attracted by a rustling sound in dry leaves. The skink, emerging onto the ledge from a cavity beneath exposed hackberry roots had its head raised high and was darting about, peering into crevices and examining its surroundings with unusual animation. After several seconds the cricket hopped into view. Possibly it had been injured already, as it moved deliberately, with short hops. Instantly the skink darted in pursuit, following its erratic course persistently, as it made several hops. In a few seconds the skink caught the cricket, bit it vigorously, and battered it against the rock ledge with violent lateral shaking. Several times the cricket was knocked from the skink's jaws, but each time it was quickly retrieved. In a few seconds its struggles were subdued, but the skink continued to worry it, dropping it and retrieving it dozens of times. The skink seized the cricket by one of the large rear legs, which was snapped off with a sudden vigorous shake. The skink then dropped and lost the detached leg, and ran back to seize the cricket again. The performance was repeated with several other legs and the antennae, until most of the appendages were eliminated and the body was softened by continued biting and chewing, Then although the cricket was of body diameter almost as great as the skink itself, the lizard swallowed it head first, engulfing it with violent gulping movements. After the front end of the prey had entered the gullet, muscles of the throat and neck were brought into play in forcing it farther down. Swallowing movements were snake-like, the lizard turning its head at right angles to the body to squeeze the morsel down.

At the pond rock pile on May 7, 1952, a small adult male was watched as it moved about over the rocks. A lycosid spider (*Pardosa lapidicina*) carrying an egg sac was basking on an inclined rock surface. When the skink had come within a few inches, it made a sudden rush at the spider which escaped easily. As this common rock-living spider can move with almost incredible speed, skinks probably do not often catch them in the open.

Captive skinks, in taking their food, seem to rely much less than some other lizards on movement of the prey as a means of detecting it. An active and hungry skink often failed to notice a spider or insect moving about on the opposite side of the terrarium a foot or more away. However, on many occasions, skinks moving about the terrarium and coming upon a motionles prey item have been seen to stop and examine it intently for several seconds, then grasp it, often in a tentative and hesitant manner, after testing it with the tongue. Sight and scent seem to be about equally important in prey recognition, each supplementing the other, and often functioning simultaneously. As many of the animals preyed upon are secretive and would seldom be found in the open by day, it seems that much of the prey is found in hiding places—in leaf litter on the forest floor, beneath flat rocks or at their edges, and in chinks and crannies of decaying logs, stumps, and tree trunks. Some of the prey animals taken are of types that are more active and swift than the skinks themselves. Presumably the olfactory sense is the more important in detecting prey that is motionless or concealed. Stebbins (1948:202) studied the nasal structure of *Eumeces*, and compared it with that of other lizards. He concluded that the extensive mucus-secreting and olfactory surfaces suggest relatively efficient humidification of inspired air and efficient olfaction in lizards of this genus. In captivity five-lined skinks thrived when provided with ample moisture and shelter and food and kept within the proper temperature range. The reactions of these captive skinks to various small animals introduced into their terraria provided clues as to their food preferences, but also were misleading in some instances. On many occasions hatchlings and young of various sizes were kept with adults of both sexes and subadults, but no instances of cannibalism were ever recorded in captivity. No hostility was seen except between adults, mainly in the breeding season. Young of the little brown skink, *Scincella laterale,* kept with adult *E. fasciatus,* and small enough to be eaten by them, likewise were unmolested. Small snakes such as *Diadophis, Carphophis,* and *Storeria* placed in terraria with the skinks evoked no strong reaction. Occasionally mild avoidance reactions were aroused but the skinks were never seen to display any hostility and readily became accustomed to such cage mates. Mealworms, the most readily available food for the captive skinks, were generally accepted by those that were hungry and sufficiently warm, but were taken with little enthusiasm. They were seldom noticed unless the skinks were within a few inches. Skinks sometimes tested them with their tongues and examined them intently then moved away without eating them. Earthworms, offered on several occasions, were not eaten. Harvestmen, seemingly of the same kind as those found in scats, were ignored by some captive individuals and taken by others but with some signs of distaste. Ants were ignored. Scarabaeid beetles, that seemed small enough to be eaten, were attacked unsuccessfully, as they were too heavily armored to be crushed in the skinks' jaws. Wasps (*Polistes*) placed in terraria were avoided, as were carabid beetles and reduviid bugs. A spider placed in the terrarium usually aroused one or more skinks to animated pursuit, as soon as it moved. Even spiders that seemed to be too large to be swallowed were sometimes pursued and attacked. Occasionally freshly killed prey was taken, especially spiders and wasp larvae. Of invertebrates minute forms are not taken, while certain ants, and various others of the kinds of insects most common on the study areas and often found rather closely associated with the skinks and using the same shelters, were never represented among the recorded food items. Carabid beetles (*Brachinus, Calosoma, Lebia, Harpalus, Pasimachus*), and reduviid bugs (*Melanolestes,* etc.) seemed to be especially abundant and available, but habitually avoided possibly because of their noxious qualities. Diptera were entirely absent from the sample in the present study—they and many other insects are so much quicker than the skinks that ordinarily these insects cannot be caught. Foliage-living insects and those that are strong and persistent fliers, are rarely available as prey.

A total of 738 food items were recorded in the present study. Arachnids with 360 items, and insects with 319, together made up 92 percent of these food items. There were 334 spiders (most were not definitely identified, but four were thomisids, 40 were lycosids, and 79 were salticids, the latter group including 27 of the genus

Phidippus); 26 harvestmen (*Leiobunum vittatum* and others); 149 orthopterans (51 ceuthophilid crickets, 31 gryllid crickets, 27 tettigoniid locusts; 17 unspecified, 14 roaches, 9 locustid grasshoppers); 80 indeterminate insects; 39 beetles (mostly carabids and scarabaeids within a narrow size range); 19 larvae (13 lepidopteran, 2 coleopteran, 1 ant, 3 indeterminate); 2 ants (*Camponotus herculaneus* and *C. castaneus*); 2 wasps; 1 moth; 1 centipede; 59 snails (31 indeterminate, 18 *Gastrocopta armifera,* 8 *Retinella electrina,* 1 *Strobilops labyrynthica,* 1 *Hawaia minuscula*); 23 sloughed skins of the skinks themselves; 2 skink eggs; and 2 skink hatchlings.

This sample is based on combined sets of data from analysis of stomach contents and of "scats." The two sets of data present somewhat divergent trends, and perhaps neither is adequately representative of the food habits in the geographic area represented. A total of 620 food items found in scats represented an average of 1.67 items per scat, whereas in 80 stomachs containing food the average was 1.44 items per stomach. Of the skinks killed and dissected more than half had empty stomachs. Many of them were, however, found inactive in shelter so that it was obvious that they had not foraged recently. Many were not killed immediately and they may have had time to digest any food in their stomachs.

Determinations of the prey down to species were possible in relatively few instances; usually only the family or the order could be determined. Those who have attempted food habits studies of insectivorous small vertebrates will appreciate the obstacles encountered. The invertebrates available to the skinks in the area of the study included many thousands of species. A large number of these species, perhaps the majority, belong to groups still not thoroughly studied, so that their taxonomy is in a state of confusion. Ordinarily the prey is crushed in the jaws and battered on the ground before ingestion; diagnostic structures are often broken or lost, making identification far more difficult. Prey animals taken are often in immature or larval stages which lack the distinguishing features presented by adults. Even the combined efforts of a team of specialists on each of the prey groups involved probably would not have sufficed to obtain generic and specific identification of every item found. In the present study, however, all determinations were made by the writer, with the aid of the small reference collection at the University of Kansas Natural History Reservation.

The 80 specimens used for stomach contents analysis nearly all came from localities off the Reservation, but all within a ten-mile radius thereof. A dozen localities were represented by these specimens, and within each locality specimens were taken in somewhat different situations. Therefore the stomach contents analyzed represents a wide range of ecological conditions, including many different microhabitats. All the stomach contents were collected in late April, May, and June—within the first half of the skinks' active season. Trends might be expected to differ in late summer and fall.

The food items from stomachs included: 38 spiders (8 of the salticid genus *Phidippus,* 5 lycosids, 4 thomisids, and the remainder unspecified); 15 insect larvae (7 of them lepidopteran and one tentatively identified as an ant, *Camponotus castaneus,* the rest unspecified); 13 unspecified insects; 10 crickets; 9 roaches; 9 snails (5 of them *Gastrocopta armifera*); 7 beetles; 4 sloughs of skinks; 3 grasshoppers; 2 grouse locusts; and one each of cave cricket (*Ceuthophilus* ?), ant (*Camponotus castaneus*), moth, centipede, sow bug, and egg of a skink. The egg was probably laid by the female that ate it, since she was found brooding an unusually small clutch of only three eggs.

The condition of food items found in stomachs varied greatly. Some were nearly intact, while others were fragmentary and represented by only a few of the more durable and indigestible parts. The larvae of various insects found in stomachs examined are especially noteworthy, since but little comparable material was found in the much larger group of items identified from scats.

The scatological material was even less satisfactory than the stomach material in providing determinable food items. The scats of these skinks are, roughly, 10 to 20 mm. long and two to four mm. in diameter, usually cylindrical and almost straight, and capped at one end with a white chalky deposit of uric acid. Superficially they have some resemblance to bird droppings, but are different in texture. The uric acid deposit is loose and crumbly, and much less compact than that with bird feces, and the food residue is much less completely disintegrated than is similar material in feces of birds. Common small snakes which might produce feces of similar size, include the ring-necked snake (*Diadophis punctatus*), the worm snake (*Carphophis amoenus*), and DeKay's snake (*Storeria dekayi*), but their feces have a much higher moisture content, lack the definite shape of the skink scats, and ordinarily do not contain readily recognizable residue of the prey. The six other species of lizards on the Reservation, the collared lizard (*Crotaphytus collaris*), brown skink (*Scincella laterale*), prairie skink (*Eumeces septentrionalis*), Sonoran skink (*E. obsoletus*), six-lined racerunner (*Cnemidophorus sexlineatus*) and glass "snake" (*Ophisaurus attenuatus*) might produce scats indistinguishable from those of the five-lined skink. However, none of these lizards except the relatively rare and secretive brown skink, occurred in either of the two situations where most of the scats were collected and it is highly improbable that the scat collection included any material from species other than the five-lined skink.

The scats consist mainly of chitinous fragments of arthropod prey. Usually the prey fragments are so well comminuted, mixed, and scattered that reconstruction is difficult. Degree of disintegration differs greatly, depending not only on the type of prey eaten, but probably also on the condition and temperature of the lizard, and the amount of other food in its digestive tract. Arthropods which have recently undergone ecdysis and have the exoskeleton still thin and soft are no doubt digested much more completely than those that have more heavily sclerotized parts. In spiders the chelicerae are more resistant to digestion than are other parts of the exoskeleton, and frequently appear, intact or nearly so, in the scat contents. The fangs being even more resistant, were sometimes found separately when no other cheliceral parts were recognizably preserved. Frequently large fragments of the carapace, with some of the eyes or all of them, were found. Spider abdomens sometimes were distinguishable, but were collapsed and compressed. Spider legs conspicuous in most of the scats, were so broken, tangled, and distorted that they were of little diagnostic value. In harvestmen, dorsal shields were nearly always fairly intact; but only small fragments of the elongate slender legs were found and they were mostly broken off when the attacking skinks battered the phalangid against the ground before swallowing it. The horny outer wings of crickets, roaches, and beetles usually were in recognizable though fragmentary condition. Occasional heads of insects often were found fairly intact. Insect legs were sometimes intact, sometimes broken into sections or crushed and fragmented. The thorax was usually represented by scattered fragments of chitin, and the abdomen by the separate chitin bands of each body segment.

Shells of snails were sometimes found nearly intact in the scats, although showing the effect of the digestive juices in their extreme brittleness. In other instances all that remained of the shell was the inner columella, and small scattered fragments.

Certain of the items eaten were probably so thoroughly digested as to leave either no hard parts at all, or minute and nondescript parts that were not recognized. The common small slug *Deroceras laeve,* for instance, would seem to be just as suitable and available for food as the various kinds of snails, but it was not recorded in either stomachs or scats. Having no hard parts except the vestigial internal shell, it probably would not be recognized in scats, even though it had been eaten. Various insect larvae, having thin outer cuticles and virtually no hard sclerotized structures except in the head, likewise probably would leave no recognizable parts. Molted skin of the skinks themselves seemed to be little altered by the digestive processes.

The collection of 371 skink scats originated mainly from two places on the Reservation nearly three-quarters of a mile apart, the pond rock pile and an old wooden bridge across a ravine. On the weathered planks of the bridge, the scats were conspicuous and could be easily gathered in quantity. At the pond rock pile, where skinks were especially abundant and were intensively studied, their scats were frequently noticed on the large rocks where they hunted and basked. A third smaller collection of scats was made in the vicinity of the laboratory buildings and adjacent rock walk fre-

Table 16. Frequency of Occurrence by Months of Various Types of Prey in a Collection of 371 Scats of Eumeces fasciatus.

	May (and April)	June	July	Aug.	Sept.	Total
Spider						
unspecified	32	32	16	100	10	190
salticid	10	18	5	31	7	71
lycosid	7	1	3	18	4	33
Harvestman (phalangid)	......	7	1	16	2	26
Orthopteran						
unspecified	......	4	......	14	......	18
cricket (ceuthophilid)	......	6	11	31	2	50
cricket (gryllid)	2	1	......	16	1	20
grouse locust	3	2	......	17	2	24
grasshopper	......	......	......	6	......	6
roach	1	2	......	2	......	5
Beetle	4	13	1	11	2	31
Ant	......	......	1	......	......	1
Wasp	1	......	......	1	......	2
Caterpillar	1	......	......	1	1	3
Other insects	3	8	6	45	5	67
Five-lined skink						
slough	2	1	3	12	1	19
hatchling	......	......	......	1	1	2
Snail						
unspecified	3	6	6	8	6	29
Gastrocopta	......	2	......	8	1	11
Retinella	1	1	......	6	......	8
Total	70	104	53	344	45	616—

quented by a few skinks. A small number of additional scats were collected elsewhere on the Reservation, but ordinarily the scats were so inconspicuous in the woodland situations where skinks occurred under typical habitat conditions, that few were found. The rock pile, bridge, and vicinity of buildings are not typical of the species' habitat and might offer somewhat different choices of prey items.

The 30 scat collections were made in 1951 and 1952. Seasonally, the sample of scats overlapped but little the sample of stomach contents, and was concentrated in the latter half of the growing season. The distribution by months was as follows: April-2; May-38; June-60; July-29; August-213; September-26. Most of the scats probably were deposited within a few days of the time they were collected, because scats disintegrate and disappear rapidly in the field where they are exposed to rain, wind and dung-feeding insects.

No clearly defined seasonal trends are revealed in Table 16 but the monthly samples, except that for August, are scarcely adequate for this purpose. Approximately equal numbers of scats were collected at the two main stations, the pond rock pile and the bridge, but some kinds of items were unequally represented in the two samples.

TABLE 17. COMPARISON OF FREQUENCY OF OCCURRENCE OF VARIOUS FOOD ITEMS IN TWO DIFFERENT SMALL AREAS, BASED ON SCAT ANALYSIS.

	Total from both collecting stations	Percentage of total in bridge sample	Percentage of total in pond rock pile sample
Spiders (all)	292	63.3	36.7
salticids	67	79.2	20.8
Phidippus audax	16	100.0	
Phidippus sp.	3		100
lycosids	33	36.3	63.7
harvestmen	28	57.1	42.9
ceuthophilids	39	30.8	69.2
grouse locusts	25	92.0	8.0
crickets	26	42.3	57.7
snail	34	61.9	38.1
Gastrocopta	11	91.0	9.0
Retinella	6	50.0	50.0

Spiders, harvestmen, and snails were well represented in both samples. In the bridge sample, salticids (especially *Phidippus audax*), grouse locusts, and the snail *Gastrocopta* were more numerous. In the rock pile sample lycosids, and especially ceuthophilid crickets were more abundant. The ceuthophilids were notably numerous among the rocks, and many of them were caught in the wire funnel traps placed there for skinks.

Little is known concerning the quantitative food requirement of any kind of lizard. Five-lined skinks fast for at least half the year during the period of dormancy, from September to April. When they emerge from dormancy in spring most of them are plump and appear to have lost little weight in the course of their long fast. In the season of activity, obviously the quantity of food consumed fluctuates according to temperature and activity of the lizard. Most of the prey taken falls within a fairly narrow size range. The prey ordinarily is swallowed entire or nearly so. This imposes a definite upper size limit. The skink of course lacks the ophidian capacity to ingest relatively enormous objects. The mental symphysis and pectoral girdle would prevent ingestion of an object much larger than the skink's body diameter, but soft-bodied and flexible arthropods of body diameter approximately equal to that of the skink may be ingested. Typical food items are of such size that from one to three of them fill the stomach to capacity. On one occasion, in an attempt to feed a brood of young recently hatched in the laboratory, I dropped into their jar a mass of newly hatched house spiders (*Theridion tepidariorum*). As these minute spiders swarmed over and around the skinks, the lizards gave little heed to them except occasionally to jerk or scratch in irritation. One skink, however, was seen to snap up a spider which ran near its snout. The adult female *Theridion* from the same web was then introduced into the skinks' jar, although it seemed too large prey for these small lizards, as its abdomen was fully as large as their body diameter. When it ran, the hatchling skinks immediately became alert and several chased it biting at it in frantic excitement. They had difficulty in grasping its smooth rounded surface, but eventually one did catch it and eat it. Full-grown mealworms averaging 26 mm. in length, and approximately .11 grams, are somewhat smaller than the usual prey of adults. In captivity hungry adult skinks took from one to nine such mealworms at a meal. However, they could not be induced to feed daily over periods of weeks, even when kept at high temperatures. Over a period of 64 days an adult male kept at approximately 80° F. in the daytime and 10 to 15 degrees lower at night, ate a total of 30 mealworms, which, in the aggregate, weighed approximately 42 per cent of his body weight. In 35 days under the same conditions an adult female ate 24 mealworms, approximately 32 per cent of her body weight.

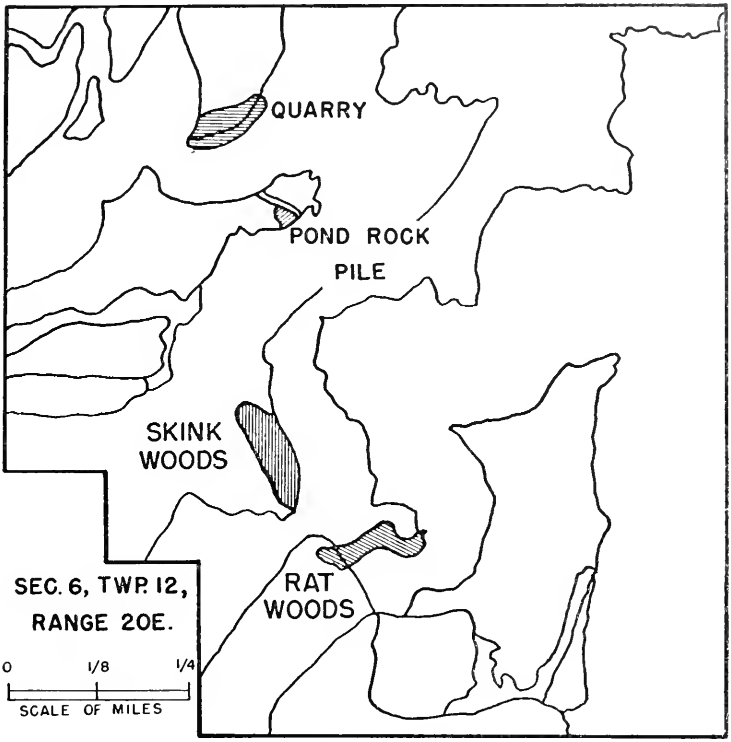

FIG. 26. Map of University of Kansas Natural History Reservation showing locations of the four study areas (shaded) where most data on five-lined skinks were obtained.

Predation and Parasitism

ESCAPE REACTIONS

Like other members of the family Scincidae, *Eumeces fasciatus* tends to be secretive in its habits and it depends on concealment rather than speed, aggressive behavior, or noxious qualities to escape its enemies. As compared with lizards in general, or with other members of the genus *Eumeces*, five-lined skinks are relatively unspecialized in their behavior, and retain a good deal of versatility. While primarily terrestrial, they are able to burrow and climb. Their reactions toward prey and natural enemies vary greatly according to circumstances.

They are less secretive than many other kinds of skinks. Nevertheless the numbers active on the ground surface at any one time, even under the most favorable weather conditions, probably are only a fraction of the total population. For instance, in two or three hours of intensive search in Skink Woods, in which almost every square yard of the area was inspected, a dozen skinks constituted an unusually good catch. Seldom were as many as 20 seen—and most of these only when uncovered in their hiding places. At the pond rock pile, often half a dozen or even more could be seen simultaneously or within the course of a few minutes, as they basked or darted about over the rock surface. These, however, represented only a small part of the number known to occur in the rock pile, which could be observed in its entirety from one spot. At other times, especially in late summer and early fall, even when weather seemed favorable, cursory search of each of the study areas failed to reveal a single individual. Presumably at such times the majority of individuals of the dense population were sheltered deep underground in relatively inaccessible hiding places. Others which escaped attention may have been climbing on tree trunks or logs, or may have been foraging on the ground but close to hiding places into which they darted undetected. The habit of "freezing" in response to a potential danger is commonly noticed in these skinks, and usually it is effective in concealing them.

Having elongate bodies and short limbs, five-lined skinks are not especially swift of foot, but the jerkiness of their movements provides compensatory elusiveness. One sufficiently warm to be fully active is nervous in its actions. Even when resting or basking it is likely to shift its position frequently, fidgeting, blinking, and panting, obviously on the alert for any sign of danger. In moving about, it usually progresses only a few steps at a time, with frequent pauses sometimes only a fraction of a second in duration. These numerous stops allow the animal to examine the terrain immediately ahead of it, and perhaps avoid blundering within reach of a lurking enemy.

Ontogenetic change in the color pattern is of significance in connection with the secretive habits. The red facial suffusion of the breeding male renders him more conspicuous in his natural surroundings, but this bright color is ephemeral. It is developed as a warning, for display to other males. Otherwise, in the adult male the color of dull brown is inconspicuous in its natural surroundings, usually against a background of leaf litter, dead stems, and soil. In the juvenile the contrasting pattern of dark brown ground-color, five longitudinal light stripes, and a vivid blue tail, is far more conspicuous. The young skink might seem to be handicapped in its chances for survival by this conspicuousness. However, in snakes it has been shown that a vivid striped pattern, characteristic of forms that are fast moving and live in dense vegetation, serves to conceal motion, and aid its possessor in confusing and eluding pursuers. The young skinks, being far more active than the adults, may use the striped pattern more effectively in this way. Often when a young skink is startled in its natural surroundings, and takes to cover, the observer does not see its outlines at all, and is conscious of it only as a flash of blue. On many occasions, while walking in the woods, I have had my attention attracted by a faint rustling of dry leaves, and have received such a fleeting impression of the flashing blue tail as to be uncertain whether or not I had actually seen a skink, until, raising a flat rock or other shelter, I found that one actually was present, concealing itself in the nearby hiding place. The erratic movements of a frightened skink that is warm and fully active, make it exceedingly elusive. With sudden lashing movements of its heavy tail and hindquarters, it may flip its body about, facing first in one direction and then in another, as it pauses before or after a rush for shelter. The sudden reversals of direction are so confusing to the pursuer that the skink may often escape by hiding after a few seconds of pursuit, even though the situation provides no shelter where the lizard is entirely secure. The tail-flip described is characteristically given at the instant the lizard reaches shelter such as a crevice, or hole, and just before it disappears. By the instantaneous pivoting of its body, throwing its tail in an arc, in the direction of its original course, the lizard creates the optical illusion of having moved beyond the point where it has taken to shelter. The peculiar writhing movements of the tail of juveniles that are moving about in the open accentuate the conspicuousness of the vividly colored tail, and suggest that this conspicuousness may be advantageous to the lizard in serving as a decoy to catch the attention of predators and distract them from the lizard itself.

In hatchlings the mortality rate is high. Tails are broken frequently in those that survive, suggesting that the tail may be useful in diverting enemies from the lizard itself. Among 121 young of the smallest sizes, (snout-vent lengths in the range of 23 to 29 mm.) 7.4 percent already had broken tails (not including, of course, those in which the tails were broken while the skinks were being captured). In slightly larger young, those in the 30-34 mm. range, perhaps averaging one month old, nearly one-fourth had lost their original tails. In those in the 35-55 mm. size class, mostly one to three months old, about half have already lost parts of their original tails. In those that are in the size group 65-69 mm. normally attained at an age of a year, approximately three-fourths have regenerated tails, and in adults the proportion with unbroken tails is even smaller—down to 16.5 percent in females of more than 75 mm. snout-vent length. In adults the incidence of broken and regenerated tails is slightly higher in females than in males. Defense of nests and sluggishness in the females during the time that they are excavating the nest burrows and guarding their eggs may result in their tails being broken more frequently.

Tree-climbing is a common means of escape and it is curious that many of those who have described the habits of *E. fasciatus* have either failed to note it at all or have minimized arboreal habits. Taylor (1936: 59) cited two instances of tree-climbing but stated: "Only rarely is this form seen in trees, at least in the western part of its range." Conant (1951: 30) stated: "They seldom climb trees, contrary to the habit of *laticeps* and *inexpectatus*." Hudson (1942: 42) mentioned seeing an adult that escaped by climbing the side of a hollow tree in southeastern Nebraska.

In the present study, tree-climbing as a means of escape was observed frequently, probably more than two hundred times in all. It was characteristic of both sexes and all ages, and was one of the commonest responses to danger. In summer when skinks were fully active, they usually moved too rapidly to be caught by hand either in the open or where they were uncovered when I turned over rocks or other shelter. To obtain specimens in any numbers at such times, an understanding was essential of the somewhat stereotyped behavior pattern involved in their escape by tree-climbing. A skink that was alarmed in the course of its foraging or basking on the ground litter was likely to run directly to the nearest tree trunk, often a distance of several or many yards, and start up it, instantly disappearing to the far side of it. The trees climbed were usually small, two to eight inches in trunk diameter; however, in the second growth forest where the study was made, large mature trees were relatively scarce. Having started up the tree trunk and concealed itself on the side opposite from its pursuer, the skink usually stopped one to five feet from the ground and waited quietly for the danger to pass. A vine of Virginia creeper, poison ivy, grape or moonseed, or a shrub such as gooseberry, providing screening foliage at the base of the tree trunk, furnished the type of sheltered situation that the skink was most likely to choose as a stopping place. The most effective technique for catching the lizard was to move slowly around the tree trunk at a distance of at least 20 or 30 feet and look for the lizard clinging to it. Having located the lizard, the collector might take careful note of its position, then return to the opposite side of the tree and approach, unseen, to close range to make a sudden grab around the trunk. This ruse often succeeded; more frequently it failed, because of the lizard's adroitness in dodging, or failure of the collector to gauge its position accurately, or a slight shifting of its position between the time it was seen and the time when an attempt was made to catch it. The response of the lizard to the unsuccessful attempt to seize it depended on whether or not it was touched, and in which direction it was driven. It might drop to the ground and burrow into leaf litter or dash away to other shelter, or it might stay on the tree trunk and spiral rapidly upward out of reach. Because of the squirrel-like tendency to keep the tree trunk between it and the pursuer, the skink usually could be relocated only after some maneuvering. Having climbed the tree trunk to the bases of the main branches, the skink usually showed little inclination to move out along them but tended to hide in the crotches or to spiral back down the trunk. Often a long stick or pole was used effectively to drive a skink back down the trunk by touching or pushing it on the upper side. A skink maneuvered to the lower part of the tree trunk was never loath to leave it in a dash for other shelter, which might be another tree trunk nearby. In moving downward or horizontally on a tree trunk or limb, a skink allows its heavy tail to bend downward from its own weight. The tail probably handicaps the lizard's climbing to some extent, and those with short regenerated tails have an advantage.

The following extracts from my field notes are selected as typical illustrations of the climbing habit as a response to danger.

September 15, 1948. A skink darted across the trail in front of me, to a tree 18 inches in diameter and climbed to a height of five feet where it stopped. Each time that I moved to approach and examine it, the skink was disturbed, and darted jerkily higher up the trunk until it was well out of reach at a height of about ten feet.

May 2, 1949. Seeing an adult male skink lying in the open, I attempted to stalk it, but it became alarmed, ran to a shagbark hickory about six inches in diameter, and soon had climbed to a height of 25 feet.

June 4, 1949. Juvenile, basking a few inches above ground on trunk of an elm ten inches in diameter, took alarm at my approach, and climbed rapidly out of reach, where it concealed itself in thick foliage.

June 22, 1949. Movement two feet above ground on an elm sapling attracted my attention; an adult male and a juvenal skink were clinging to the trunk only a few inches apart, and neither moved as I approached and examined them from a distance of less than three feet. The concealment afforded by numerous short twigs with thick foliage apparently caused them to feel secure.

September 21, 1949. A juvenile was noticed climbing eight feet above the ground on a locust trunk. As I approached the skink continued upward to a height of approximately 15 feet above the ground where it disappeared around the trunk and could not be relocated.

July 7, 1950. A nearly grown juvenile ran to an elm sapling four inches in diameter, and climbed up out of reach. When the skink reached the main crotch, it turned facing downward alertly. By reaching up with a long stick and poking it on the hindquarters, I succeeded several times in chasing it part way down the trunk, but each time it ran back up to the crotch and returned to the same position.

July 26, 1950. A hatchling uncovered beneath a flat rock ran to a nearby oak tree about four inches in diameter and climbed to a height of five feet before it was caught. An adult female seen foraging in the open ran to a dead shrub and climbed one of the stems, inclined at an angle of about 45°. Ascending this stem she was unable to get more than three feet above the ground, and was easily captured. Another adult female seen foraging in the open ran to an oak about three inches in diameter, climbed rapidly to a height a little more than a foot above the ground, and concealed herself under the stem of a poison ivy vine twined about the tree trunk.

July 27, 1951. A female brooding her eggs dashed out of the nest when the flat rock covering it was lifted, ran 15 feet to a hickory sapling and climbed it.

May 1, 1952. An adult male found beneath a rock ran to a small tree ten feet away, climbed up on the opposite side, and stopped about a foot above the ground. My first attempt to seize it failed and it ran around the trunk and stopped at a height of four feet. The next try was likewise unsuccessful, and the skink dropped to the ground and burrowed into leaf litter.

May 15, 1952. An adult male startled as it basked in a patch of sunlight in thick woods, dashed 25 feet without stopping, to an osage orange tree and disappeared behind the base of the trunk. Moving to the far side of the tree I located the skink clinging to the trunk two feet above the ground. My attempt to catch it failed and it spiralled up the trunk to a height of ten feet. When I poked at it with a stick, it crouched close to the trunk allowing the stick almost to touch it, then it spiralled down the trunk and could not be relocated.

June 23, 1952. When I struck the trunk of a partly dead ailanthus tree with a brush knife to determine whether it was hollow, a juvenile darted out of a cavity five feet above the ground, ran farther up the trunk, and disappeared into another small hole. An adult male was seen running across the vertical wall of a building, clinging to the rough asphalt siding. When it was alarmed it ran to a crevice and hid.

A more unusual escape-reaction was observed on May 25, 1952, at Tonganoxie State Lake, by Sydney Anderson, who recorded that a skink, alarmed by him at the edge of the water dived and hid among submerged rocks. Similarly, Boyer and Heinze (1934: 194) record of this species, in Jefferson County, Missouri: "When pursued they do not hesitate to take to the water and are very agile swimmers over short distances at least." Parker (1948: 25) wrote that in western Tennessee *fasciatus* sometimes showed a preference for habitat in the vicinity of water, and, if other concealment was not available, it would usually take refuge in the water.

NATURAL ENEMIES

Little is known concerning the kinds of predators that destroy five-lined skinks, or their importance in its ecology. In studies of the food habits of various predatory birds and mammals, workers often have been interested chiefly in items of direct economic bearing, and have tended to lump as "lizard" or "reptile" material that might have included *Eumeces fasciatus.* I have been able to find only a few specific references to predation on it. Nevertheless many kinds of predators probably utilize it as food, at least occasionally. Owls probably seldom have opportunity to prey on these skinks, which are not known to be active after dark. Nestling broad-winged hawks observed in 1954 were found to have eaten an adult and a subadult five-lined skink on June 13 and June 23. The Cooper's hawk and red-shouldered hawk also are probable predators as both are known to feed upon small reptiles. Mammalian predators which might be expected to take skinks occasionally include the red fox, gray fox, bobcat, mink, weasels, skunks, opossum, armadillo, moles, and shrews. Snakes, especially those of the genera *Elaphe, Lampropeltis, Cemophora, Micrurus* and *Ancistrodon,* may include some of the chief predators on the skink. Certain larger lizards also may prey upon it.

Of these several potential predators, only the opossum, armadillo, and snakes (*Elaphe obsoleta, E. guttata, Lampropeltis triangulum, L. calligaster, L. getulus,* and *Ancistrodon contortrix*), Sonoran skink and the greater five-lined skink (in confinement) have actually been recorded as preying on *Eumeces fasciatus* but circumstantial evidence has been obtained for the mole (*Scalopus aquaticus*) and short-tailed shrew (*Blarina brevicauda*). The short-tailed shrew may be one of the major predators on the skink. This shrew prefers the same habitats and occurs throughout the skink's extensive range. Like the skink, it is a characteristic inhabitant of the hardwood forests of the eastern United States, but its range extends farther north and west. A high proportion of the skinks examined had scars, usually on the sides or dorsal surface of the body, or of the tail near its base—wounds which must have been made by a small, sharp-toothed animal. For example, in May

1951, eighteen per cent of 155 skinks captured on the study areas had such scars. The incidence seemed to vary according to age and possibly sex; the scars were present in 22.9 per cent of the adult males, 25.5 per cent of the adult females, and only 9.8 per cent of the yearlings (these three groups being represented by approximately equal numbers in the sample). As the scars are more or less permanent, adults could be expected to show a much higher incidence than young. Females, being inclined to stay in their nest burrows and defend them against small predators, may receive more wounds than the males, which are quicker to escape. None of the invertebrates present on the study area is sufficiently large or powerful to inflict such wounds, and none of the birds, reptiles, or amphibians has a dentition capable of producing them. The wood mouse (*Peromyscus leucopus*) is the most abundant small mammal in the skink's habitat; other rodents present in relatively small numbers include the prairie vole (*Microtus ochrogaster*), harvest mouse (*Reithrodontomys megalotis*) and pine vole (*Microtus pinetorum*). Both voles and harvest mice have been known to kill skinks caught in the same traps with them, but individuals experimentally placed with skinks in captivity have failed to molest them and it seems likely that the attacks in traps were motivated by extreme hunger or self defense. The irregular scars from lacerated wounds characteristic of the skinks bear little similarity to rodent bites, in which the long, sharp-edge incisors make slit-like punctures. Other small mammals abundant in the places where skinks were studied were the insectivores: the common mole, short-tailed shrew, and least shrew (*Cryptotis parva*).

On one occasion when a large five-lined skink was put in a terrarium with a recently captured short-tailed shrew, each displayed strong aversion for the other. The skink crouched, attempting to conceal itself in the end of the terrarium farthest from the shrew, and resisted efforts to drive it toward the shrew. In exploring the terrarium the shrew several times sensed the skink's presence, and then scampered away in frantic haste. The skink also rushed away several times when the shrew came close enough to disturb it. Three days later, when the shrew had become accustomed to the terrarium, the test was repeated, with different results. The shrew, having finished the food left for it, was noticed moving about the terrarium, sniffing and testing objects with its tactile snout, obviously hungry and searching for more food. The skink was then dropped near it. In a few seconds the shrew sensed the skink's presence and pounced upon it, and bit hard on its back. The skink reacted with a violent flexure of its body which caused the shrew to release it instantly, and both rushed away in opposite directions. After a few seconds the shrew located the skink again, and moved up to it with little hesitation but with nervous alert sniffing, and delivered another quick bite after which the two separated as before, the skink showing signs of injury. Soon the shrew attacked a third time, and bit the skink's tail severing it near the base. As the skink rushed away, the detached tail performed lively squirming movements, but the shrew seized it, held it down, and began to eat the exposed flesh on the broken end as the tail writhed. After rapid nibbling it would drop the tail, and leaving it temporarily would explore the terrarium. Several times on these trips it encountered the skink and renewed its attack. As death of the skink seemed imminent, it was then removed, and it survived with no apparent ill effects. The wounds inflicted by the shrew bore close resemblance to those noticed on skinks in the wild. It seemed almost certain that *Blarina* had inflicted most of these wounds or all of them. On subsequent occasions several other captive shrews that were tested, quickly killed and ate skinks that were introduced into their containers. The least shrew, *Cryptotis,* likewise occurred in all situations where skinks were taken, and in some localities was more abundant than the larger *Blarina.* Bites inflicted by these two kinds of shrews might be indistinguishable, but because of its larger size, *Blarina* would seem by far the more formidable enemy.

Reynolds (1945:367) found *E. fasciatus* to be the most frequent reptile in a collection of opossum scats from Missouri, with two occurrences in 100 fall scats and ten occurrences in 100 spring scats. Sandidge (1953: 98 and 101) recorded one of these skinks among numerous other items identified from stomach contents of sixty-six opossums. Probably the opossum is a frequent predator on this skink. Although no specific instances were obtained on the area of the study, flat rocks a few inches in diameter frequently have been found flipped over, larger ones and those solidly anchored in the ground have been found partly undermined by opossums scratching away the loose dirt at their edges. The rocks found disturbed by opossums were typical of those used as shelter by the skink. On many occasions wire funnel traps set for skinks and other reptiles along hilltop rock ledges were found to have been disturbed, either shifted in position or with their rock shelters removed, or rolled downhill or broken open. Similarly, heavy flat rocks used to cover pitfalls, to protect the small animals falling into them from predators, often were found to have been shifted somewhat, or completely removed. When such raids became frequent and troublesome, steel traps were set beside the reptile traps to discourage the raiders or catch them and determine their identity. On several occasions opossums were caught and somewhat less frequently, spotted skunks (*Spilogale interrupta*). These skunks probably prey regularly on lizards including the five-lined skink. However no definite records were obtained. Crabb (1941: 356-358) in his food habits study of the spotted skunk in southeastern Iowa, did not record this or any other species of reptile among the items identified in 834 scats. On the Reservation both opossums and skunks were, in many instances, attracted to the reptile traps by the insects and other arthropods in them, rather than by lizards. The striped skunk (*Mephitis mephitis*) is another of the predators which probably feeds upon the five-lined skink occasionally on this area.

In the contents of 103 armadillo stomachs collected in west-central Louisiana, in 1947 and 1948 I found the broken tail of one *Eumeces fasciatus.* The lizard itself evidently had escaped (Fitch, 1949a: 88). Many clutches of lizard eggs were found in the contents of the armadillo stomachs and some of these probably were eggs of *Eumeces*, which are similar to those of other small lizards in the same region (*Anolis carolinensis, Sceloporus undulatus*) in size, shape, and color.

Among 217 identified prey items from stomachs and scats of Sonoran skinks (*Eumeces obsoletus*) from northeastern Kansas were remains of three hatchling five-lined skinks. Taylor (1953b: 212) recorded that a *Eumeces laticeps* shipped from Arkansas to Kansas ate an *E. fasciatus* that was with it in the container. Several authors have recorded predation on *Eumeces fasciatus* by snakes of various kinds in captivity. Conant (1951: 211) recorded that one was eaten by a blacksnake (*Coluber constrictor*) placed in the collecting sack with it. Anderson (1942: 211 and 216) recorded that a king snake (*Lampropeltis getulus holbrooki*) and a young copperhead (*Ancistrodon contortrix*) each fed upon them. Hurter (1911: 184) recorded that a milk snake, *Lampropeltis triangulum syspila,* placed in a bucket with a *Eumeces fasciatus* was found swallowing it a short time later and its tail had been broken off.

Ruthven (1911: 268) mentioned that stomachs of milk snakes, *L. t. triangulum,* collected in Michigan contained remains of five-lined skinks. Ditmars (1907: 352) wrote that stomachs of several *L. t. elapsoides* contained *Eumeces,* and Wright and Bishop (1915: 167) wrote of the same kind of king snake in the Okefinokee Swamp region: "It feeds on ground lizards, skinks, swifts, and other snakes and lizards."

Mr. Richard B. Loomis is of the opinion that the five-lined skink is one of the chief food sources for the milk snake (*L. t. syspila*). Having kept many of these snakes in captivity and experimentally offered them different types of prey, he found that individuals inclined to feed would avidly seize and eat skinks and young mice, but other proffered prey, small adult rodents, snakes, or lizards other than *Eumeces* were either rejected or were taken with some hesitation. These milk snakes have habitat preferences similar to the skink, which would seem to be one of the most available food sources. Loomis recorded in his field notes that a juvenal blotched king snake (*L. calligaster*) 310 mm. in total length, taken on April 8, 1950, seven miles southwest of Tulsa, Oklahoma, had eaten a large adult *E. fasciatus*. Another juvenal blotched king snake that he found under a flat rock near Sunflower, Johnson County, Kansas, regurgitated an adult five-lined skink. Loomis also recorded a juvenal rat snake (*Elaphe guttata emoryi*) and a juvenal pilot black snake (*E. obsoleta*) each feeding on individuals of *Eumeces fasciatus* in captivity. Uhler, Cottam and Clarke (1939: 622) in a study of the contents of the alimentary tracts of 893 snakes of 18 species, from the George Washington National Forest, Virginia, found among the prey items only one skink (species undetermined but most probably *E. fasciatus*). It had been eaten by one of the two corn snakes (*Elaphe guttata*) that were examined in the study.

On June 11, 1950, in Skink Woods, a young copperhead 335 mm. in snout-vent length and weighing 27.6 grams, had a gravid female skink in its stomach. Another young copperhead (335 mm., 36.1 grams) trapped near Rat Woods on August 28, 1953, had in its stomach a bob-tailed adult five-lined skink. Many copperheads collected on the Reservation were kept in captivity for short periods, and from them a total of 44 scats were obtained, each scat containing the remains of one or more prey animals eaten in the wild. Of this total, five scats contained remains of *Eumeces fasciatus*, which was one of the more frequent items, although small mammals collectively made up the bulk of the scat contents.

PARASITES

Skinks, like many other lizards, are likely to be infested with parasites. Little attention was devoted to the endoparasites in the present study, but they were noted from time to time. On several occasions small nematodes and flukes were seen in feces voided by lizards which were handled. Small white cysts were seen in the body cavities of several that were dissected.

Harwood (1932: 65) examined for endoparasites nine *E. fasciatus* along with many other reptiles and amphibians collected near Houston, Texas. Most of them were infested and five kinds of helminths were identified. Two of the skinks were infested with *Oswaldocruzia pipiens,* a spirurid nematode that was also present in various other lizards, snakes, toads and frogs from the same region; four had *Comocercoides dukae,* an oxyurid nematode also present in various lizards, snakes, turtles, and frogs; one had in its intestine *Oochoristica eumecis,* named as a new species by Harwood, and found only in *Eumeces;* one contained *Cysticercus* sp. in its body cavity, present in great abundance as white globular structures .6 mm. in diameter (Harwood states that possibly these were larvae of *Oochoristica*). One skink contained *Mesocoelium americanum,* a dicrocoelid trematode which was found also in the brown skink (*Scincella laterale*) and DeKay's snake (*Storeria dekayi*).

The ectoparasites of these skinks consist mainly of chiggers. Wharton (1952: 135) lists three species; *Trombicula alfreddugesi, T. splendens,* and *T. gurneyi.* The first species is the common pest chigger of humans and domestic animals in the United States, and south through tropical America. Wharton lists 136 known hosts which are fairly evenly divided among mammals, birds and reptiles; he lists four kinds of frogs and toads. *Trombicula splendens* is a similar and closely related species which has been recorded from thirty-eight vertebrate hosts including mammals, birds, reptiles, and a tree-toad. *Trombicula gurneyi* belongs to a separate subgenus and it was originally recorded from *Eumeces fasciatus* which seems to be one of the principal hosts.

Two of these mites, *T. alfreddugesi* and *T. gurneyi,* were on skinks collected on the Reservation, and nearby areas. A four year study of the chiggers in this general region by Loomis (MS), Wolfenbarger (1953) and Kardos (MS) has clarified the ecological relationships of the several kinds of chiggers present, including their local distribution with respect to vegetation, soil type, moisture and temperature, host preferences, and seasonal occurrence. At the quarry, Rat Woods and the pond rock pile, the chigger population consisted chiefly of *T. alfreddugesi,* while at Skink Woods *T. gurneyi* was also abundant. In some local situations where they are among the most abundant of vertebrates the skinks probably are important as hosts of *T. gurneyi.* An individual skink may have dozens of chiggers on it at one time but usually there are fewer.

There are several favorable sites of attachment. The most favored site is in the axilla. There the scales are minute and granular with exposed areas of thin and tender skin, and the chiggers are well protected from dessication and are not likely to be rubbed off as the skink moves about. Other favorite sites of attachment are: about the insertion of the hind limb, about the cloacal opening, on the eyelids and on the toes. Only occasionally are chiggers found attached on the dorsal surface. When attached in protected spots in the tender skin of the axilla or groin, they are often in dense clusters of a dozen or more. Damage to the skin resulting from the attachment of the first chiggers renders conditions more favorable for the attachment of others. At Rat Ledge and at the quarry, many of the larger Sonoran skinks (*Eumeces obsoletus*) were captured, and individuals were far more heavily infested than were *E. fasciatus* from the same places. A single Sonoran skink might be found to have hundreds of chiggers, widely distributed over its body with concentrations at the axillae, groins, lateral neck region, and any injured spots where the protective armor of scales was broken. The reasons for the greater susceptibility of *E. obsoletus* are not entirely clear. It is a larger, less active species with coarser scalation, and is more subterranean in its habits.

The chiggers that attach to skinks seem to occasion but little discomfort. There is no local swelling and inflammation such as occurs in humans. The infestations observed in five-lined skinks were not sufficiently severe to cause debilitation or any noticeable symptoms. There is, however, a possibility that chiggers are vectors of microorganisms causing diseases in reptiles, just as they are for certain mammals (including humans) in some parts of the world.

Bishopp and Trembley (1935:42) record a single kind of tick, *Ixodes ricinus scapularis* Say, the black-legged tick, as parasitic in its immature stages on *Eumeces fasciatus.* This tick, however, has been recorded principally from mammals, of which many kinds serve as hosts for its larval, nymphal, and adult stages.

Population

COMPOSITION

Population structure obviously differs from place to place and from time to time. Because of the differences in secretiveness and elusiveness between young and adults and between males and females, true sex ratios and age ratios are obscured. In the period of weeks between the emergence from hibernation and the onset of the breeding season, these skinks tend to be less secretive than at other times, and secondary sexual and age differences in behavior are minimized. A sample at this season should be more representative of the true population composition than samples taken at other times of year. In a sample of 308 skinks available for the month of April, including the collections made on the Reservation and on nearby areas, in 1949, 1950, 1951, and 1952, 36.7 per cent were adult males, 28.3 per cent were adult females, and 35.0 per cent were young. That these figures cannot, however, be accepted as an accurate indication of the population composition is shown by the data from the areas where intensive population studies were made. Data are most complete from Skink Woods. For 292 adults taken there over a four year period, the sex ratio was 100:122.6. On this area after the first year of study a substantial proportion of the individuals recorded were repeaters from one year to the next, and in some cases for three or even four successive years. Many could be definitely assigned to a known age group. By analogy the majority of others could be tentatively assigned with some assurance on the basis of measurements, and relatively few were of indeterminate status. By assigning each of these indeterminate individuals to one or another age group, on the basis of greatest probability, the approximate composition of the population could be determined. Of 611 adults, 55 per cent were "two-year olds" (in the season between their second and third hibernations, which was their first breeding season). The percentage was not significantly different in the two sexes.

On the average, a pair of adults produces somewhat more than nine eggs per year. From the time individuals of a brood start their development in the egg until they are breeding adults two years later, they undergo such drastic reduction in numbers that, on the average, approximately only one per brood survives. Most of the mortality probably occurs early, especially before hatching, also in the inexperienced hatchlings, and in the first hibernation. In spring, after emergence from hibernation, young are generally taken in smaller numbers than are adults. Their relative scarcity is only apparent, owing to greater secretiveness, and greater elusiveness when found. In spring, newly matured adults (age class about 21 months) may be taken in somewhat larger numbers than young (age class about 9 months). The latter obviously must be more numerous, in a stable population however, as the 21 month age class necessarily has sustained some loss since it was 9 months old.

Success of the annual brood varies greatly from year to year, depending on the weather and various other factors. In 1949 evidently conditions were near optimum; young hatched early and were especially numerous in late summer. In 1950 these young hatched in 1949 made up 40 per cent of the total catch (excluding hatchlings) in Skink Woods and were relatively more numerous than young of the corresponding age group in other years. In 1951, these young of the 1949 brood, grown to adults, made up 70 per cent of the breeding populations, as against 36 per cent for the corresponding class in 1950 and 58 per cent for the corresponding class in 1952.

Even after attainment of adulthood, any given age group evidently is subject to annual reduction amounting to at least half its numbers. Within six or seven years, at the most, the original numbers would be reduced to an insignificant percentage. At an age of four or five years individuals probably have attained their maximum size, with obscured pattern and changed proportions suggestive of advanced age. Occasional individuals possibly attain much greater age, but certainly few live more than five years. Like most small animals, the five-lined skink has a short life expectancy and a rapid population turnover. As compared with mammals of comparable sizes, the small rodents and insectivores that are this lizard's community associates and are subject to many of the same hazards, the skink is notably successful, with a much longer life expectancy. For these small mammals the life span is seldom as long as a year. Most kinds of small birds likewise have a life expectancy less than that of the five-lined skink, although somewhat greater than that of small mammals.

DENSITY

The population density changes constantly, following an annual cycle with gradual reduction to its lowest ebb in late June or early July, then rapid increase to a high point a few weeks later when hatching of the single annual brood has been completed. In a normally successful breeding season the population is at least doubled, but reproductive success varies from year to year, as the population responds to weather conditions that are favorable or unfavorable, even where the environment remains fairly stable. In most places, however, local populations continue upward or downward trends for periods of years in response to successional changes which cause progressive improvement or deterioration of local habitats. Local populations are likely to be more or less isolated from others by areas where the habitat does not exist. Even in an area of favorable habitat such as a wooded hillside of several acres, the population is not at all evenly distributed, but concentrations occur along rock outcrops, and about decaying logs, or stone piles. In intervening areas lacking such abundant shelter, and less productive of food, the population is sparse, or there may be no permanent residents.

In view of these traits, and the difficulty of obtaining a representative sample, no precise measurements of population density can be made. During the time required to secure a sample, the population undergoes change. At the pond rock pile, an area of approximately .05 acre, the skinks were found in remarkably high concentrations, 57 in 1949, 85 in 1950, 37 in 1951, and 51 in 1952. These numbers represent population densities of, respectively, 1120 per acre, 1960 per acre, 746 per acre, and 1000 per acre. No such concentrations were found elsewhere, and probably do not occur in natural habitat. The Skink Woods study area of 2¼ acres is typical of favorable habitat in the region of the study, and the numbers taken there are more significant. For 1949 the 74 skinks recorded comprise an incomplete sample, and the population density of 33 per acre represented is certainly somewhat too low. For other years the following population densities (exclusive of hatchlings) are indicated: 1950, 92 per acre; 1951, 61 per acre; 1952, 49 per acre. These figures are only approximate, of course, and it is difficult to judge how accurately they reflect the true numbers. Even the most intensive collecting may be insufficient to obtain every individual on a small area. Within each season there are shifts of range by some individuals, off the study area and corresponding shifts onto it by others, so that the numbers caught in the course of an entire season are somewhat too high. The individuals taken on the study area may regularly range beyond its boundaries to some extent, so that the seeming population density is somewhat too high. Actually this was probably a minor source of error for the Skink Woods study area, as nearly half its perimeter was bordered by an open field uninhabitable for the skinks, and the remaining perimeter adjoined areas much less favorable than the central portion.

Census of the population of the study area by a ratio such as the "Lincoln Index" used in game management studies was scarcely practicable because of the changing seasonal habits distorting the recorded ratios of the sexes and of age groups somewhat differently at different stages of the season. These changing ratios tend to produce an erroneously high population figure, unless separate computations are made from the data for adult males, adult females, and young. Census figures obtained by this method were erratic but seemed to bear out in a general way, the population figures based on total numbers of individuals taken.

In favorable habitat where they occur in high populations of 50 to 100 per acre in spring, these lizards must attain a biomass of a pound or more per acre. Biomass in a population probably fluctuates but little during the course of the annual cycle, even though the number of individuals changes greatly. The steady elimination of individuals through various mortality factors, is compensated for by rapid growth of the young.

Summary

Five-lined skinks were studied for four consecutive years in four small areas, totalling approximately ten acres, on the University of Kansas Natural History Reservation, Douglas County, Kansas. The information gained from intensive study on these areas has been supplemented by data from skinks collected elsewhere in northeastern Kansas, and from an extensive literature pertaining to this species.

The genus *Eumeces,* to which the common five-lined skink belongs, has more than 50 species, occurring throughout Central America, North America to the latitude of southern Canada, and, in the Old World, across southern Asia and North Africa. Within the genus, the five-lined skinks, comprising a dozen species, form a natural group of closely related forms. In this "*fasciatus* group" nine of the species occur in the Orient, Japan and neighboring islands and the adjacent mainland. The remaining three, including *E. fasciatus,* occur in the eastern United States. Specific differences are to be found in details of pattern, scalation, and size, and, in some instances, they were long unrecognized. *E. fasciatus* coincides closely in its distribution with the Deciduous Forest Biome of southeastern North America. An early Tertiary deciduous forest in Alaska and probably in the Bering Strait area, evidently growing in a humid, mild-temperate climate, included genera of plants that are now most characteristic of southeastern North America along with other kinds now characteristic of forest remnants in southeastern Asia, and still others characteristic of the western United States. The *fasciatus* group seemingly dispersed from a northern center that may have coincided with the early Tertiary deciduous forest of Alaska.

Eumeces laticeps almost coincides in distribution with *E. fasciatus,* but does not occur quite so far north, and unlike *fasciatus* it occurs throughout Florida. Young are similar in appearance but *laticeps* is a larger, more powerful species, notably arboreal in its habits. *E. inexpectatus* much more closely resembles *fasciatus,* and ecological divergence is slight. It is characteristic of hot and dry rocky areas in open woods, and is more southern in distribution, although there is extensive overlap with *fasciatus* and *inexpectatus* shares nearly all of its range with *laticeps.*

Eumeces fasciatus is most abundant in well-drained, open, rocky situations within its forest habitat. It is scarce or absent in bottomland forest that is subject to flooding and requires a forest with openings in the leaf canopy so that sunshine patches for basking are available. In northeastern Kansas, at least, woodlands that are browsed by livestock, and have scanty undergrowth, provide better habitat than those that are protected. *E. fasciatus* is likely to be most abundant in cutover woodland, and may reach greatest numbers in artificial situations, such as old rock piles, or the vicinity of deserted sawmills. In the north, the species is increasingly confined to open situations, while in the south it may inhabit heavily wooded areas. An abundant supply of moisture is a necessity and the species is limited to a climate of high humidity. Dew normally supplies the source of drinking water, without which the skinks rapidly become emaciated and die. Optimum body temperature was determined to be near 34° C., from a series of temperature readings taken both under natural conditions and in confinement under conditions permitting behavioral thermoregulation. By thermoregulatory behavior, active skinks in the wild tend to maintain their body temperatures near this level over a wide range of environmental temperatures. They can tolerate body temperatures only a few degrees higher, but, within a range of several degrees below 34° C., efficiency is little impaired and incentive to make readjustment is slight. At progressively lower temperatures skinks become slower and less efficient. They are, however, capable of copulation at temperatures down to 21° C., and of feeding at 16° C. At 10° C. they are slow and clumsy, barely capable of normal locomotion. At temperatures near freezing they are torpid; they can survive temperatures a little below freezing, but cannot survive being frozen solid. More than half the year is spent in hibernation in northeastern Kansas. Weight loss is slight during hibernation.

Normally the skinks emerge from hibernation in early April in northeastern Kansas, several weeks earlier in the southern states and correspondingly later in the northern part of the range. Maximum activity occurs in the period of weeks following emergence, interrupted from time to time by cold weather which necessitates return to torpidity. After approximately three weeks of activity the adults attain breeding condition. Breeding males acquire a salmon red suffusion of the head region. They become pugnacious and fight on sight. Fighting does not involve territorial defense. In confinement males may mutilate or kill each other. In their search for females, and fighting, the breeding males are so much more active and conspicuous than they are at other times of year that published descriptions usually refer to males as red-headed, with no cognizance of the fact that this condition exists for only a few weeks in the annual cycle. Old adult males lose the striped pattern and blue color of the tail of the young, and are golden brown, usually a little darker on the sides. Males find females by a combination of sight and scent. Sexual relations are promiscuous, and there is but little courtship behavior. The male pursues the female and grasps in his jaws loose skin at or behind her shoulder region, and maintains this hold during copulation which lasts about five minutes. Within a few days after insemination, usually in early May, females become actively hostile to males. In late May or early June the gravid females become unusually secretive and excavate nest burrows in damp soil under flat rocks, or in rotten wood of decaying logs and stumps. The single annual clutch of eggs is laid in June. The average clutch is somewhat more than nine eggs, with larger and older females slightly exceeding younger and smaller females in average productivity. The female remains in the nest burrow with her clutch most of the time, from laying until after hatching. She alters the nest burrow, dampens it in time of drought, keeps the cavity from being filled with loose soil, prevents the eggs from adhering to the sides or floor of the cavity, and she may repulse certain small predators capable of destroying the eggs if they were left undefended. When they are laid, the eggs are approximately 11 x 7½ mm. and weigh .4 grams or a little less. By hatching time they have enlarged to 15 x 11 mm. and each weighs about a gram. Recorded incubation periods vary from 27 days to 47 days; development of the embryo is slowed at low temperatures, and eggs experimentally kept in a refrigerator at 11° to 12° C. for periods of days hatched later than others of the same clutch that developed under normal conditions, indicating that development was almost halted in the eggs kept at such low temperatures. Eggs are, however, tolerant of a wide range of temperature, and can develop in nearly dry soil, or can survive partial submersion in water for at least two days. Under weather conditions prevailing in 1951, incubation periods of about six weeks were recorded. Incubation may be shortened by retention of ova in the oviducts in early stages of embryonic development. Hatching may occur from the first week of July to mid-August, but in any one year most clutches hatch within two weeks of each other. Hatching of eggs in a clutch extends over a day or two. The hatchling gradually becoming active inside the egg, slits the leathery shell with its egg tooth, and spends several hours in the early stages of emergence. After resting with head and shoulders protruding, becoming adjusted to the outside environment and gaining strength, it lunges from the egg. For a day or two after hatching, the young remains in the nest, being slow and feeble, and handicapped in its movements by the protruding belly distended by the yolk mass. The female usually remains in the nest cavity for a day or two after the eggs hatch, showing affinity for the young by curling around them protectively. Family ties are broken as soon as the young leave the nest, and they do not return. Hatchlings average a little less than an inch in snout-vent length, and have a sharply defined five-lined pattern on a black ground color, and vivid blue tail. Hatchlings make rapid growth in late summer, and by the time of their retirement into hibernation, the more successful may have doubled in length, and may have increased their original weight, of approximately .3 or .4 grams, more than eight-fold. After emergence from their first hibernation the young continue their rapid growth. When they are a year old, some of them are as large as small adults. However, they can usually be distinguished from adults by the more sharply defined pattern. These grown young retain the hatchling pattern but the contrast between stripes and ground color, and between body and tail is not quite so sharp. Especially in those with regenerated tails, the vivid blue of the hatchling's tail has become much dulled. By the time they retire to their second hibernation, the young have mostly grown to small adult size. A small percentage are retarded in their growth and fail to mature. Upon emergence from their second hibernation, the grown young mature sexually and participate in the annual breeding season, in early May, and they may comprise the majority of breeding adults. The ratio of new adults to old adults however varies from year to year depending on the varying fortunes of successive annual broods. The new adults overlap older ones in size, but are usually distinguishable on the basis of their coloration, as they retain the striped body pattern (dulled, especially on the head) and with distinctly blue color on the tail. In skinks that are three years old or more, the dorsal stripes have become obscured and partly blended with the ground color, which becomes progressively paler with advancing age. Metamorphosis is most complete in old males, which retain no trace of the stripes or of the blue color on the tail. Old females usually retain the dark lateral area, and the tail is usually bluish gray, with a blue scale remaining here and there if the tail has not been regenerated.

Most individuals lose their original tails, however. By the time the young are approximately two months old, about half have had their tails broken, and by the time they are a year old and have grown to small adult size, three-fourths have regenerated tails. Some individuals may have had their tails broken and regenerated many times. Tails regenerate rapidly and most of the growth is made within the first few weeks. The regenerated tail is not so long as the original lost portion.

Individuals tend to stay within small areas which are their regular home ranges. These ranges are only a fraction of an acre in extent, but vary considerably in size and shape according to the individual and the situation. Home ranges of approximately 90-foot diameter for adult males and young, and a little more than 30-foot diameter for adult females are indicated. A home range generally centers about some environmental feature providing shelter and food, such as a log, hollow tree, or rock outcrop. Activity tends to be concentrated in the central part of the home range. An individual may continue to occupy the same home range throughout its lifetime, or it may gradually alter its range, shifting by slow stages into a new area. Some individuals seem to "get lost" or voluntarily shift, and settle in a new area which may be hundreds of feet removed from the original range. Shifts are most likely to occur after emergence from hibernation, when the lizard finds its habitat somewhat altered. Individuals released in areas strange to them settled down and established new home ranges, either immediately or after brief wandering.

The five-lined skink is a predator, occasionally taking small vertebrates (lizards and possibly newborn mice) but depending for most of its food on invertebrates. Of these it takes a wide variety. Spiders are the mainstay of the diet, and various salticids and lycosids are the kinds most frequently preyed upon. Phalangids are also eaten. Of insects, orthopterans (including roaches, ceuthophilid and gryllid crickets, grouse locusts, and small grasshoppers) are most important in the food. Larvae of moths and both larvae and adults of beetles are also taken in quantity. Small snails make up an important part of the diet, and the skinks often eat their own sloughed skins. Less frequently taken food items include certain large ants, centipedes, moths, and miscellaneous insects. Rarely the adult skinks may even eat eggs or young of their own species.

Prey is found by sight and scent, and consists of almost any small animals within a certain size range (small enough to be swallowed entire, but large enough to make up a substantial part of a meal) of types which are not too heavily armored, lack noxious defensive secretions, and live on or in the ground or decaying wood. They are ordinarily crushed in the jaws or battered against the ground, and then swallowed entire.

Natural enemies of the five-lined skink certainly include the broad-winged hawk and probably other kinds of hawks and also include various predatory mammals such as the opossum, armadillo, skunks, moles and shrews; snakes (the copperhead, milk snake, king snake, corn snake, and probably others), the Sonoran skink and even the closely related but larger *Eumeces laticeps*. On the Reservation, the short-tailed shrew was certainly the commonest, and probably by far the most important natural enemy. A high proportion of the skinks examined had scars resembling those inflicted by shrews experimentally confined with skinks in captivity. In time of danger escape reactions vary according to the type of enemy and the attending circumstances. Frequently an alarmed skink may escape into a hole or crevice, running directly to it from a distance of several yards. Under other circumstances a skink may burrow into ground litter of dry leaves and other debris, or may even dive and hide underwater. One of the commonest escape reactions is climbing tree trunks. It occurs even in gravid females that are slow and clumsy, being weighed down with eggs. Generally the skink stays on the main trunk of the tree, attempting to conceal itself by utilizing the screening vegetation that is available. In the young, especially, the bright blue tail seems to be used as a decoy, for it is carried, arched high and waved conspicuously as the lizard moves about. Rapid lashing movements of the conspicuous tail as the animal darts erratically for shelter may serve to confuse a pursuer, at least as to the direction that the skink has taken.

This skink is parasitized by various helminths, both cestodes and nematodes, which inhabit the digestive tract and body cavity. Some of these infest many kinds of amphibian and reptilian hosts, but others may be confined to the five-lined skink. Their life cycles, and effect upon the host are not well known. Ectoparasites consist principally of chiggers. Three kinds have been recorded on the skinks; *Trombicula alfreddugesi, T. splendens,* and *T. gurneyi*. The first two are common pest chiggers which attack humans as well as a wide variety of other mammalian, avian and reptilian hosts. *T. gurneyi* is a less common species found mainly on *Eumeces fasciatus* and confined to its woodland habitat.

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25-3559

(Continued from inside of front cover)

24. Geographic range of the hooded skunk, Mephitis macroura, with description of a new subspecies from Mexico. By E. Raymond Hall and Walter W. Dalquest. Pp. 575-580, 1 figure in text. January 20, 1950.
25. Pipistrellus cinnamomeus Miller 1902 referred to the Genus Myotis. By E. Raymond Hall and Walter W. Dalquest. Pp. 581-590, 5 figures in text. January 20, 1950.
26. A synopsis of the American bats of the Genus Pipistrellus. By E. Raymond Hall and Walter W. Dalquest. Pp. 591-602, 1 figure in text. January 20, 1950.

Index. Pp. 605-638.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. *1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr. and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.

Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. 1. Preliminary survey of a Paleocene faunule from the Angels Peak area, New Mexico. By Robert W. Wilson. Pp. 1-11, 1 figure in text. February 24, 1951.
2. Two new moles (Genus Scalopus) from Mexico and Texas. By Rollin H. Baker. Pp. 17-24. February 28, 1951.
3. Two new pocket gophers from Wyoming and Colorado. By E. Raymond Hall and H. Gordon Montague. Pp. 25-32. February 28, 1951.
4. Mammals obtained by Dr. Curt von Wedel from the barrier beach of Tamaulipas, Mexico. By E. Raymond Hall. Pp. 33-47, 1 figure in text. October 1, 1951.
5. Comments on the taxonomy and geographic distribution of some North American rabbits. By E. Raymond Hall and Keith R. Kelson. Pp. 49-58. October 1, 1951.
6. Two new subspecies of Thomomys bottae from New Mexico and Colorado. By Keith R. Kelson. Pp. 59-71, 1 figure in text. October 1, 1951.
7. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.
8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.
9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.
*10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202, 68 figures in text. December 15, 1951.
11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.
12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.
13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.
14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15. 1951.
15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.
17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.
18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White, Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.

(Continued on back of cover)

(Continued from inside of back cover)

21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-337. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
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34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
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Index. Pp. 647-676.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.
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3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
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Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 2 pls., 26 figs. in text, 17 tables. September 1, 1954.

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Myology and Serology of the Avian Family Fringillidae, A Taxonomic Study

BY

WILLIAM B. STALLCUP

UNIVERSITY OF KANSAS
LAWRENCE
1954

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9. Additions to the list of the birds of Louisiana. By George H. Lowery, Jr. Pp. 177-192. November 7, 1947.
10. A check-list of the birds of Idaho. By M. Dale Arvey. Pp. 193-216. November 29, 1947.
11. Subspeciation in pocket gophers of Kansas. By Bernardo Villa R. and E. Raymond Hall. Pp. 217-236, 2 figures in text. November 29, 1947.
12. A new bat (Genus Myotis) from Mexico. By Walter W. Dalquest and E. Raymond Hall. Pp. 237-244, 6 figures in text. December 10, 1947.
13. Tadarida femorosacca (Merriam) in Tamaulipas, Mexico. By Walter W. Dalquest and E. Raymond Hall. Pp. 245-248, 1 figure in text. December 10, 1947.
14. A new pocket gopher (Thomomys) and a new spiny pocket mouse (Liomys) from Michoacán, México. By E. Raymond Hall and Bernardo Villa R. Pp. 249-256, 6 figures in text. July 26, 1948.
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(Continued on inside of back cover)

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CONTENTS

PAGE

INTRODUCTION 160

MYOLOGY OF THE PELVIC APPENDAGE 162
  General Statement 162
  Materials and Methods 163
  Description of Muscles 164
  Discussion of Myological Investigations 175

COMPARATIVE SEROLOGY 185
  General Statement 185
  Preparation of Antigens 186
  Preparation of Antisera 188
  Methods of Serological Testing 188
  Experimental Data 190
  Discussion of Serological Investigations 190

CONCLUSIONS 201

SUMMARY 208

LITERATURE CITED 210

INTRODUCTION

The relationships of many groups of birds within the Order Passeriformes are poorly understood. Most ornithologists agree that some of the passerine families of current classifications are artificial groups. These artificial groupings are the result of early work which gave chief attention to readily adaptive external structures. The size and shape of the bill, for example, have been over-emphasized in the past as taxonomic characters. It is now recognized that the bill is a highly adaptive structure and that it frequently shows convergence and parallelism.

Since studies of external morphology have failed in some cases to provide a clear understanding of the relationships of passerine birds, it seems appropriate that attention be given to other morphological features, to physiological features, and to life history studies in an attempt to find other clues to relationships at the family and subfamily levels.

This paper reports the results of a study of the relationships of some birds of the Family Fringillidae and is based on the comparative myology of the pelvic appendage and on the comparative serology of saline-soluble proteins. Where necessary for comparative purposes, birds from other families have been included in these investigations.

It has long been recognized that the Fringillidae include dissimilar groups. Recent work by Beecher (1951b, 1953) on the musculature of the jaw and by Tordoff (1954) primarily on the structure of the bony palate has emphasized the artificial nature of the assemblage although these authors disagree regarding major divisions within it (see below).

The Fringillidae have been distinguished from other families of nine-primaried oscines by only one character—a heavy and conical bill (for crushing seeds). Bills of this form have been developed independently in several other, unrelated, groups; as Tordoff (1954:7) has pointed out, *Molothrus* of the Family Icteridae, *Psittorostra* of the Family Drepaniidae, and most members of the Family Ploceidae have bills as heavy and conical as those of the fringillids. The ploceids are distinguished from the fringillids by a single external character: a fairly well-developed tenth primary whereas in fringillids the tenth primary is absent or vestigial. Tordoff (1954:20) points out, however, that this distinction is of limited value since in other passerine families the tenth primary may be present in some species of a genus and absent in others. The Genus

Vireo is an example. Furthermore, at least one ploceid (*Philetairus*) has a small, vestigial tenth primary, whereas some fringillids (*Emberizoides,* for example) possess a tenth primary which is rather large and ventrally placed (Chapin, 1917:253-254). Thus, it is obvious that studies based on other features are necessary in order to attain a better understanding of the relationships of the birds involved.

Sushkin's studies (1924, 1925) of the structure of the bony and horny palates have served as a basis for the division of the Fringillidae into as many as five subfamilies (Hellmayr, 1938:v): Richmondeninae, Geospizinae, Fringillinae, Carduelinae, and Emberizinae.

Beecher (1951b:280) points out that "the richmondenine finches arise so uninterruptedly out of the tanagers that ornithologists have had to draw the dividing line between the two groups arbitrarily." His study of pattern of jaw-musculature substantiates this. He states further that the cardueline finches arise without disjunction from the tanagers. He suggests, therefore, that the two groups of "tanager-finches" be made subfamilies of the Thraupidae and that a third subfamily be maintained for the more typical tanagers. He states that the emberizine finches are of different origin, arising from the wood warblers (1953:307). Beecher (1951a:431; 1953:309) includes the Dickcissel, *Spiza americana,* in the Family Icteridae, chiefly on the basis of jaw muscle-pattern and the horny palate.

Tordoff (1954:10-11) presents evidence that the occurrence of palato-maxillary bones in nine-primaried birds indicates relationship among the forms possessing them. He points out that all fringillids except the Carduelinae possess palato-maxillaries that are either free or more or less fused to the prepalatine bar. He points out also that in all carduelines, the prepalatine bar is flared at its juncture with the premaxilla, and that the mediopalatine processes are fused across the midline; noncardueline fringillids lack these characteristics. In addition to the above he cites differences between the carduelines and the "other" fringillids in the appendicular skeletons, in geographic distribution, in patterns of migration, and in habits. Tordoff concludes, therefore, that the carduelines are not fringillids but ploceids, their closest affinities being with the ploceid Subfamily Estrildinae. On the basis of palatal structure, the Fringillinae and Geospizinae are combined with the Emberizinae, the name Fringillinae being maintained for the subfamily. The tanagers merge with the Richmondeninae on the one hand and with the Fringillinae on the other. On this basis, Tordoff (1954:32) suggests that the Family

Fringillidae be divided into subfamilies as follows: Richmondeninae, Thraupinae, and Fringillinae. The carduelines are placed as the Subfamily Carduelinae in the Family Ploceidae.

From the foregoing, it is apparent that the two most recent lines of research have given rise to conflicting theories regarding relationships within the Family Fringillidae. The purpose of my investigation, therefore, has been to gather information, from other fields, which might clarify the relationships of these birds.

Since the muscle pattern of the leg in the Order Passeriformes is thought to be one of long standing and slow change, any variation which consistently distinguishes one group of species from another could be significant. With the hope that such variation might be found, a study of the comparative myology of the legs was undertaken.

The usefulness of comparative serology as a means of determining relationship has been demonstrated in many investigations. Its use in this instance was undertaken for several reasons: comparative serology has its basis in biochemical systems which seem to evolve slowly; its methods are objective; and its use has, heretofore, resulted in the accumulation of data which seem compatible, in most instances, with data obtained from other sources.

I acknowledge with pleasure the guidance received in this study from Prof. Harrison B. Tordoff of the University of Kansas. I am indebted also to Prof. Charles A. Leone without whose direction and assistance the serological investigations would not have been possible; to Professors E. Raymond Hall and A. Byron Leonard whose suggestions and criticisms have been most helpful in the preparation of this paper; and to T. D. Burleigh of the U. S. Fish and Wildlife Service for gifts of several specimens used in this work. Assistance with certain parts of the study were received from a contract (NR163014) between the Office of Naval Research of the United States Navy and the University of Kansas.

Myology of the Pelvic Appendage

General Statement

In an excellent paper in which the muscles of the pelvic appendage of birds are carefully and accurately described, Hudson (1937) reviewed briefly the more important literature pertaining to the musculature of the leg which had been published to that date. A review of such information here, therefore, seems unnecessary.

Myological formulae suggested by Garrod (1873, 1874) have been extensively used by taxonomists as aids in characterizing the orders of birds. Relatively few investigations, however, involving the comparative myology of the leg have been undertaken at family and subfamily levels. The works of Fisher (1946), Hudson (1948), and Berger (1952) are notable exceptions.

The terminology for the muscles used in this paper follows that of Hudson (1937), except that I have followed Berger (1952) in Latinizing all names. Homologies are not given since these are reviewed by Hudson. Osteological terms are from Howard (1929).

Materials and Methods

Specimens were preserved in a solution of one part formalin to eight parts of water. Thorough injection of all tissues was necessary for satisfactory preservation. Most of the down and contour feathers were removed to allow the preservative to reach the skin.

In preparing specimens for study, the legs and pelvic girdle were removed and washed in running water for several hours to remove much of the formalin. They were then transferred to a mixture of 50 per cent alcohol and a small amount of glycerine.

All specimens were dissected with the aid of a low power binocular microscope. Where possible, several specimens of each species were examined for individual differences. Such differences were found to be slight, involving mainly size and shape of the muscles. The size is dependent partly on the age of the bird, muscles from older birds being larger and better developed. The shape of a muscle (whether long and slender or short and thick) is due in part to the position in which the leg was preserved; that is to say, a muscle may be extended in one bird and contracted in another. For these reasons, descriptions and comparisons are based mainly on the origin and insertion of a muscle and on its position in relation to adjoining muscles.

Birds dissected in this study are listed below (in the order of the A. O. U. Check-List):

SPECIES

Vireo olivaceus (Linnaeus)
Seiurus motacilla (Vieillot)
Passer domesticus (Linnaeus)
Estrilda amandava (Linnaeus)
Poephila guttata (Reichenbach)
Icterus galbula (Linnaeus)
Molothrus ater (Boddaert)
Piranga rubra (Linnaeus)
Richmondena cardinalis (Linnaeus)
Guiraca caerulea (Linnaeus)
Passerina cyanea (Linnaeus)
Spiza americana (Gmelin)
Hesperiphona vespertina (Cooper)
Carpodacus purpureus (Gmelin)
Pinicola enucleator (Linnaeus)
Leucosticte tephrocotis (Swainson)
Spinus tristis (Linnaeus)
Loxia curvirostra Linnaeus
Chlorura chlorura (Audubon)
Pipilo erythrophthalmus (Linnaeus)
Calamospiza melanocorys Stejneger
Chondestes grammacus (Say)
Junco hyemalis (Linnaeus)
Spizella arborea (Wilson)
Zonotrichia querula (Nuttall)
Passerella iliaca (Merrem)
Calcarius lapponicus (Linnaeus)

Description of Muscles

The descriptions which follow are those of the muscles in the leg of the Red-eyed Towhee, *Pipilo erythrophthalmus*. Differences between species, where present, are noted for each muscle. The term thigh is used-to refer to the proximal segment of the leg; the term crus is used for that segment of the leg immediately distal to the thigh.

Musculus iliotrochantericus posticus (Fig. 2).—The origin of this muscle is fleshy from the entire concave lateral surface of the ilium anterior to the acetabulum. The fibers converge posteriorly, and the muscle inserts by a short, broad tendon on the lateral surface of the femur immediately distal to the trochanter. It is the largest muscle which passes from the ilium to the femur.

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliotrochantericus anticus (Fig. 3).—Covered laterally by the *m. iliotrochantericus posticus*, this slender muscle has a fleshy origin from the anteroventral edge of the ilium between the origins of the *m. sartorius* anteriorly and the *m. iliotrochantericus medius* posteriorly. The *m. iliotrochantericus anticus* is directed caudoventrally and inserts by a broad, flat tendon on the anterolateral surface of the femur between the heads of the *m. femorotibialis externus* and *m. femorotibialis medius* and just distal to the insertion of the *m. iliotrochantericus medius.*

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliotrochantericus medius (Fig. 3).—Smallest of the three *iliotrochantericus* muscles, this bandlike muscle has a fleshy origin from the ventral edge of the ilium just posterior to the origin of the *m. iliotrochantericus anticus.* The fibers are directed caudoventrally, and the insertion is tendinous on the anterolateral surface of the femur between the insertion of the other two *iliotrochantericus* muscles.

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliacus (Figs. 4, 5).—Arising from a fleshy origin on the ventral edge of the ilium just posterior to the origin of the *m. iliotrochantericus medius,* this small slender muscle passes posteroventrally to its fleshy insertion on the posteromedial surface of the femur just proximal to the origin of the *m. femorotibialis internus.*

Action.—Moves femur forward and rotates it posteriorly.

Comparison.—No significant differences among the species studied.

Musculus sartorius (Figs. 1, 4).—A long, straplike muscle, the *sartorius* forms the anterior edge of the thigh. The origin is fleshy, half from the anterior edge of the ilium and from the median dorsal ridge of this bone and half from the posterior one or two free dorsal vertebrae. The insertion is fleshy along a narrow line on the anteromedial edge of the head of the tibia and on the medial region of the patellar tendon.

Action.—Moves thigh forward and upward and extends shank.

Comparison.—In *Loxia* and *Spinus*, only one-third of the origin is from the last free dorsal vertebra. In *Hesperiphona, Carpodacus, Pinicola,* and *Leucosticte,* only one-fifth of the origin is from this vertebra.

Musculus iliotibialis (Fig. 1).—Broad and triangular, this muscle covers most of the deeper muscles of the lateral aspect of the thigh. The middle region is fused with the underlying *femorotibialis* muscles. In the distal half of this muscle there are three distinct parts; the anterior and posterior edges are fleshy and the central part is aponeurotic. The origin is from a narrow line along the iliac crests—from the origin of the *m. sartorius*, anteriorly, to the origin of the *m. semitendinosus* posteriorly. The origin is aponeurotic in the preacetabular region but fleshy in the postacetabular region. The distal part of the muscle is aponeurotic and joins with the *femorotibialis* muscles in the formation of the patellar tendon. This tendon incloses the patella and inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus.

Action.—Extends crus.

Comparison.—In *Vireo* the central aponeurotic portion of this muscle is absent.

Musculus femorotibialis externus (Fig. 2).—Covering the lateral and anterolateral surfaces of the femur, this large muscle has a fleshy origin from the lateral edge of the proximal three-fourths of the femur. The origin separates the insertion of the *m. iliotrochantericus anticus* from that of the *m. ischiofemoralis* and, in turn, is separated from the origin of the *m. femorotibialis medius* by the insertions of the *m. iliotrochantericus anticus* and *m. iliotrochantericus medius*. Approximately midway of the length of the femur this muscle fuses anteromesially with the *m. femorotibialis medius*. Distally, the *m. femorotibialis externus* contributes to the formation of the patellar tendon which inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus.

Action.—Extends crus.

Comparison.—No significant differences noted among the species studied.

Musculus femorotibialis medius (Figs. 2, 4).—The origin of this muscle, which lies along the anterior edge of the femur, is fleshy from the entire length of the femur proximal to the level of attachment of the proximal arm of the biceps loop. Laterally this muscle is completely fused for most of its length with the *m. femorotibialis externus* and contributes to the formation of the patellar tendon, which inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus. Many of the fibers, nevertheless, insert on the proximal edge of the patella.

Action.—Extends crus.

Comparison.—No significant differences noted among the species studied.

Musculus femorotibialis internus (Fig. 4).—One of the most superficial muscles lying on the medial surface of the thigh, this muscle is divided, especially near the distal end, into two parts, lateral and medial. The origin of the lateral part is fleshy from a line on the medial surface of the femur; the origin begins proximally at a point near the insertion of the *m. iliacus*. The medial, bulkier part of the muscle has a fleshy origin on the medial surface of the lower one-third of the femur. The two parts fuse to some extent above the points of insertion and insert on the medial edge of the head of the tibia.

Action.—Rotates tibia anteriorly.

Comparison.—Two parts of this muscle variously fused; otherwise, no significant differences in the species studied.

Musculus piriformis (Fig. 3).—This muscle is represented by the *pars caudi-*

femoralis only, the *pars iliofemoralis* being absent in passerine birds as far as is known. The *pars caudifemoralis* is flat, somewhat spindle-shaped, and passes anteroventrally from the pygostyle to the femur. The origin is tendinous from the anteroventral edge of the pygostyle, and the insertion is semitendinous on the posterolateral surface of the shaft of the femur about one-fourth its length from the proximal end.

Action.—Moves femur posteriorly and rotates it in this direction; moves tail laterally and depresses it.

Comparison.—No significant differences noted among the species studied.

Musculus semitendinosus (Figs. 2, 3, 5).—The origin from the extreme posterior edge of the posterior iliac crest of the ilium is fleshy and is aponeurotic from the last vertebra of the synsacrum and the transverse processes of several caudal vertebrae. The straplike belly passes along the posterolateral margin of the thigh. Immediately posterior to the knee, the muscle is divided transversely by a ligament. That portion passing anteriorly from the ligament is the *m. accessorius semitendinosi* (here considered a part of the *m. semitendinosus*) and is discussed below. The ligament continues distally in two parts; one part inserts on the medial surface of the *pars media* of the *m. gastrocnemius* and the other part fuses with the tendon of insertion of the *m. semimembranosus.*

The *m. accessorius semitendinosi* extends anteriorly from the above mentioned ligament to a fleshy insertion on the posterolateral surface of the femur immediately proximal to the condyles.

Action.—Moves femur posteriorly, flexes the crus and aids in extending the tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus semimembranosus (Figs. 3, 4, 5).—This straplike muscle passes along the posteromedial surface of the thigh. The origin is semitendinous along a line on the ischium, from a point dorsal to the middle of the ischiopubic fenestra to the posterior end of the ischium, and from a small area of the abdominal musculature posterior to the ischium. The insertion is by means of a broad, thin tendon on a ridge on the medial surface of the tibia immediately distal to the head of this bone. The tendon of insertion passes between the head of the *pars media* and *pars interna* of the *m. gastrocnemius* and is fused with the tendon of the *m. semitendinosus.*

Action.—Flexes crus.

Comparison.—No significant differences noted among the species studied.

Musculus biceps femoris (Fig. 2).—Long, thin, and somewhat triangular, this muscle lies on the lateral side of the thigh just underneath the *m. iliotibialis.* Its origin is from a line along the anterior and posterior iliac crests underneath the origin of the *m. iliotibialis.* Anterior to the acetabulum the origin is aponeurotic, and the edge of this aponeurosis passes over the proximal end of the femur. The origin posterior to the acetabulum is fleshy. The most anterior point of origin is difficult to ascertain but it lies near the center of the anterior iliac crest. The most posterior point of origin is immediately dorsal to the posterior end of the ilioischiatic fenestra. Behind the knee the fibers of this muscle converge to form the strong tendon of insertion which passes through the biceps loop, under the tendon of origin of the *m. flexor perforatus digiti II,* and inserts on a small tubercle on the posterolateral edge of the fibula at the point of the tibia-fibula fusion.

The biceps loop is tendinous and the distal end attaches to a protuberance on the posterolateral edge of the femur at the proximal edge of the external condyle. The proximal end attaches to the anterolateral edge of the femur immediately proximal to the distal end of the loop, which extends posterior to the femur. The distal arm of this loop is connected with the tendon of origin of the *m. flexor perforatus digiti II* by a strong tendon.

Action.—Flexes crus.

Comparison.—No significant differences noted among the species studied.

Musculus ischiofemoralis (Fig. 3).—Short and thick, this muscle arises directly from the lateral surface of the ischium between the posterior iliac crest and the ischiopubic fenestra. The area of origin extends to the posterior edge of the ischium. The insertion is tendinous on the lateral surface of the trochanter opposite the insertion of the *m. iliotrochantericus medius.*

Action.—Moves femur posteriorly and rotates it in this direction.

Comparison.—No significant differences noted among the species studied.

Musculus obturator internus (Figs. 4, 7).—Lying on the inside of the pelvis and covering the medial surface of the ischiopubic fenestra, is this flat, pinnate, leaf-shaped muscle. The origin is fleshy and is from the ischium and pubis around the edges of this fenestra; none of the fibers arises from the membrane stretched across the fenestra. Anteriorly the fibers converge and form a strong tendon that passes through the obturator foramen and inserts on the posterolateral surface of the trochanter of the femur.

Action.—Rotates femur posteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus obturator externus (Fig. 7).—Short and fleshy, this muscle consists of two parts which are not easily separable but which may be traced throughout its length. The parts are more nearly distinct at the origin. The dorsal part arises directly from the ischium along the dorsal edge of the obturator foramen. The larger ventral part arises directly from the anterior and ventral edges of the obturator foramen. The fibers of the dorsal part pass anteriorly, cover the tendon of the *m. obturator internus* laterally, and insert on the trochanter around the point of insertion of the latter muscle. The fibers of the ventral part pass parallel with the tendon of the *m. obturator internus* and insert on the trochanter immediately distal and posterior to the tendon of the latter muscle.

Action.—Rotates femur posteriorly.

Comparison.—In *Passer, Estrilda, Poephila, Hesperiphona, Carpodacus, Pinicola, Leucosticte, Spinus* and *Loxia,* this muscle is undivided and, in its position, origin, and insertion, resembles the ventral part of the bipartite muscle described above. The origin is from the anterior and ventral edges of the obturator foramen and the insertion is on the trochanter of the femur immediately distal and posterior to the insertion of the *m. obturator internus.* In all other genera examined, the muscle is bipartite. In *Chlorura* the dorsal part is larger and better developed than it is in the other genera.

Musculus adductor longus et brevis (Figs. 3, 4, 5).—Consisting of two distinct, straplike parts, this large muscle lies on the medial surface of the thigh, posterior to the femur.

The *pars anticus* has a semitendinous origin on a line that extends posteriorly from the posteroventral edge of the obturator foramen to a point half way across the membrane that covers the ischiopubic fenestra. The insertion is fleshy along the posterior surface of the femur from the level of the insertion of the *m. piriformis* distally to the medial surface of the internal condyle.

The *pars posticus* originates by a broad, flat tendon on a line across the posterior half of the membrane that covers the ischiopubic fenestra. The insertion is at the point of origin of the *pars media* of the *m. gastrocnemius* on the posteromedial surface of the proximal end of the internal condyle of the femur. There is a broad tendinous connection with the proximal end of the *pars media* of the *m. gastrocnemius.* The anterior edge of the *pars posticus* is overlapped medially by the posterior edge of the *pars anticus.*

Action.—Flexes thigh; may flex crus also and may extend tarsometatarsus.

Comparison.—In *Vireo olivaceous,* the origin of this muscle does not extend the length of the ischiopubic fenestra. The origin, furthermore, is along the dorsal edge of the ischiopubic fenestra and not from the membrane covering the fenestra. Finally, in this species, the origin of the *pars posticus* is fleshy.

Musculus tibialis anticus (Figs. 2, 5).—Lying along the anterior edge of the crus, a part of this muscle is covered by the *m. peroneus longus.* The origin is by two distinct heads, each of which is pinnate. The anterior head arises directly from the edges of the outer and inner cnemial crests. The posterior head arises by a short, strong tendon from a small pit on the anterodistal edge of the external condyle of the femur. This tendon and the proximal end of the muscle pass between the head of the fibula and the outer cnemial crest. The two heads of the muscle fuse at a place slightly more than one-half of the distance down the crus. At the distal end of the crus this muscle gives rise to a strong tendon which passes under a fibrous loop immediately proximal to the external condyle in company with the *m. extensor digitorum longus* and which passes between the condyles of the tibia and inserts on a tubercle on the anteromedial edge of the proximal end of the tarsometatarsus.

Action.—Flexes tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus extensor digitorum longus (Figs. 3, 5, 8).—Slender and pinnate, this muscle lies along the anteromedial surface of the tibia. The origin is fleshy from most of the region between the cnemial crests and from a line along the anterior surface of the proximal fourth of the tibia. Approximately two-thirds of the distance down the crus the muscle gives rise to the tendon of insertion which passes through the fibrous loop near the distal end of the tibia in company with the *m. tibialis anticus.* The tendon then passes along beneath the supratendinal bridge at the distal end of the tibia, traverses the anterior intercondylar fossa, and passes beneath a bony bridge on the anteromedial surface of the proximal end of the tarsometatarsus. The tendon continues along the anterior surface of the tarsometatarsus to a point immediately above the bases of the toes and there gives rise to three branches, one to the anterior surface of each foretoe. The insertions of each branch are on the anterior surfaces of the phalanges as shown in Fig. 8.

Action.—Extends foretoes.

Comparison.—This muscle is weakly developed in *Leucosticte* and *Calcarius;* the belly is slender and extends only half way down the crus before giving rise to the tendon of insertion. The functional significance of this variation is difficult to understand. The convergence in muscle pattern shown by these two genera, however, is in all probability the result of similarities in behavior patterns. These birds perch less frequently than do the other birds studied. Thus, the toes are neither flexed nor extended as often; the smaller size of the *m. extensor digitorum longus* may have resulted in part from this lessened activity. Except for the variations just noted, there are no significant differences among the species studied; even the rather complex patterns of insertion are identical.

Musculus peroneus longus (Fig. 1).—Relatively thin and straplike, this muscle lies on the anterolateral surface of the crus and is intimately attached to the underlying muscles. The part of the origin from the proximal edges of the inner and outer cnemial crests is semitendinous but the part of the origin from the lateral edge of the shaft of the fibula is tendinous. Approximately two-thirds the distance down the crus the muscle gives rise to the tendon of insertion. Immediately above the external condyle of the tibiotarsus this tendon divides. The posterior branch inserts on the proximal end of the lateral edge of the tibial cartilage. The anterior branch passes over the lateral surface of the external condyle to the posterior surface of the tarsometatarsus and there unites with the tendon of the *m. flexor perforatus digiti III.*

Action.—Extends tarsometatarsus and flexes third digit.

Comparison.—No significant differences noted among the species studied.

Musculus peroneus brevis (Figs. 2, 3).—Lying along the anterolateral surface of the tibia, this slender, pinnate muscle arises from a fleshy origin along this surface and along the anterior surface of the fibula from a point immediately proximal to the insertion of the *m. biceps femoris* to a point approximately two-thirds of the way down the crus. Near the distal end of the tibia the muscle gives rise to the tendon of insertion that passes through a groove on the anterolateral edge of the tibia just above the external condyle. Here the tendon is held in place by a broad fibrous loop and passes under the anterior branch of the tendon of insertion of the *m. peroneus longus* and inserts on a prominence on the lateral edge of the proximal end of the tarsometatarsus.

Action.—Extends tarsometatarsus and may abduct it slightly.

Comparison.—No significant differences noted among the species studied.

Musculus gastrocnemius (Figs. 1, 4).—The largest muscle of the pelvic appendage, it covers superficially all of the posterior surface, most of the medial surface, and half of the lateral surface of the crus. The muscle originates by three distinct heads.

The *pars externa* covers the posterolateral surface of the crus, is intermediate in size between the other two heads, and arises by a short, strong tendon from a small bony protuberance on the posterolateral side of the distal end of the femur immediately proximal to the fibular condyle. The tendon is intimately connected with the distal arm of the loop for the *m. biceps femoris.*

The *pars media* is the smallest of the three heads and lies on the medial surface of the crus. The head of the *pars media* is separated from the *pars interna* by the tendon of insertion of the *m. semimembranosus* and originates by a short, strong tendon from the posteromedial surface of the proximal end of the internal condyle of the femur. The proximal portion of the *pars media* has tendinous connections with the tendon of the *m. semitendinosus* and with the *pars posticus* of the *m. adductor longus et brevis.*

The *pars interna* is the largest of the three heads and covers most of the medial surface of the crus. This head in its proximal portion is distinctly divided into anterior and posterior parts, the former overlapping the latter medially. The origin of the posterior part is fleshy from the anterior half of the tibial head. Some of the fibers of the anterior part arise directly from the inner cnemial crest while its remaining fibers arise from the patellar tendon (Fig. 1) and form a band that extends around the anterior surface of the knee, covering the insertion of the *m. sartorius.*

Approximately half way down the crus, the three heads give rise to the tendon of insertion, the *tendo achillis,* which passes over and is tightly bound to the posterior surface of the tibial cartilage. The insertion is tendinous on the posterior surface of the hypotarsus and along the posterolateral ridge of the tarsometatarsus. This tendon seems to be continuous with a fascia which forms a sheath around the posterior surface of the tarsometatarsus holding the other tendons of this region firmly in the posterior sulcus.

Action.—Extends tarsometatarsus.

Comparison.—Study of the *pars externa* and *pars media* reveals no significant differences among the species dissected. The *pars interna,* however, is subject to some variation which is described below.

Pars interna bipartite

Vireo
Seiurus
Icterus
Molothrus
Piranga
Richmondena
Guiraca
Passerina
Spiza
Chlorura
Pipilo
Calamospiza
Chondestes
Junco
Spizella
Zonotrichia
Passerella
Calcarius

The two parts of the *m. gastrocnemius* are most distinct in *Vireo. Icterus, Molothrus, Richmondena, Guiraca,* and *Passerina* lack the fibrous band that passes around the front of the knee. In *Spiza* this band of fibers is smaller than in the other species.

Pars interna undivided

Passer
Estrilda
Poephila
Hesperiphona
Carpodacus
Pinicola
Leucosticte
Spinus
Loxia

In *Leucosticte,* although the *pars interna* is undivided, there is a band of fibers which extends around the front of the knee (see discussion, p. 183).

Musculus plantaris (Fig. 5).—Small and slender, this muscle lies on the posteromedial surface of the crus, beneath the *pars interna* of the *m. gastrocnemius* and originates by fleshy fibers from the posteromedial surface of the proximal end of the tibia immediately distal to the internal articular surface. The belly extends approximately one-sixth of the way down the crus and gives rise to a long, slender tendon that inserts on the proximomedial edge of the tibial cartilage.

Action.—Extends tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus flexor perforatus digiti II (Figs. 3, 9).—This is a slender muscle which lies on the lateral side of the crus beneath the *pars externa* of the *m. gastrocnemius* and is intimately connected anteromedially with the *m. flexor digitorum longus* and posteromedially with the *m. flexor hallucis longus.* The origin is by a strong tendon from the lateral surface of the external condyle of the femur at the point of origin of the *m. flexor perforans et perforatus digiti II.* This tendon serves also as the origin of the anterior head of the *m. flexor hallucis longus.* The tendon connects also by a broad tendinous band with the distal arm of the loop for the *m. biceps femoris* and by a similar band with the lateral edge of the fibula immediately distal to the head. The tendon of insertion passes distally, perforates the tibial cartilage near its lateral edge, traverses the middle medial canal of the hypotarsus (Fig. 6), and passes distally to the foot. At the distal end of the tarsometatarsus the tendon is held against the medial surface of the first metatarsal by a straplike sheath. The tendon then passes over a sesamoid bone between the first metatarsal and the base of the second digit and is bound to this bone by a sheath. The tendon inserts mainly along the posteromedial edge of the proximal end of the first phalanx of the second digit, although the termination is sheathlike and covers the entire posterior surface of this phalanx. This sheathlike termination is perforated by the tendons of the *m. flexor perforans et perforatus digiti II* and the branch of the *m. flexor digitorum longus* that inserts on the second digit.

Action.—Flexes second digit.

Comparison.—In *Vireo* this muscle is larger and more deeply situated than it is in the other species examined and has no connection with the *m. flexor hallucis longus.*

Musculus flexor perforatus digiti III (Fig. 5).—Long and flattened, this muscle lies on the posteromedial side of the crus beneath the *m. gastrocnemius.* The belly is tightly fused laterally with the belly of the *m. flexor hallucis longus* and posteriorly with the belly of the *m. flexor perforatus digiti IV.* The origin is by a long, strong tendon from a small tubercle just medial to, and at the proximal end of, the external condyle of the femur. Below the middle of the crus this muscle terminates in a strong tendon which perforates the tibial cartilage near its lateral edge. In this region the tendon is sheathlike and wrapped around the tendon of the *m. flexor perforatus digiti IV.* These two tendons together pass through the posterolateral canal of the hypotarsus (Fig. 6). Immediately distal to the hypotarsus the two tendons separate, and the tendon of the *m. flexor perforatus digiti III* receives a branch of the tendon of the *m. peroneus longus.* The tendon passes distally over the surface of the second trochlea, and its insertion is sheathlike on the posterior surface of the first phalanx, and on the proximal end of the second. In the area of insertion this tendon is perforated by that of the *m. flexor perforans et perforatus digiti III* and by that of the *m. flexor digitorum longus* to the third digit.

Action.—Flexes digit III.

Comparison.—In *Passer, Estrilda, Poephila, Hesperiphona, Carpodacus, Pinicola, Leucosticte, Spinus,* and *Loxia* the edges of the sheathlike tendon are thickened at the points of insertion, so that the tendon appears to have two branches which insert along the posterolateral edges of the first phalanx and are connected medially by a fascia.

Musculus flexor perforatus digiti IV (Fig. 3).—Extending along the posterior edge of the crus, this slender muscle lies beneath the *m. gastrocnemius.* The belly is fused with those of the *m. flexor hallucis longus* and *m. flexor perforatus digiti III.* Its origin is fleshy from the intercondyloid region of the distal end of the femur and has a few fibers arising from the tendon of origin of the *m. flexor perforatus digiti III.* Near the distal end of the crus the muscle gives rise to the strong tendon of insertion which perforates the tibial cartilage near its lateral edge and in this region is ensheathed by the tendon of the *m. flexor perforatus digiti III.* The two tendons pass together through the posterolateral canal of the hypotarsus (Fig. 6). The tendon continues distally along the tarsometatarsus and the posterior surface of digit IV. The tendon bifurcates at approximately the middle of the first phalanx. A short lateral branch inserts on the posterolateral edge of the proximal end of the second phalanx. The long medial branch is perforated by a branch of the *m. flexor digitorum longus;* the distal end is flattened, has thickened edges, and inserts over the posterior surfaces of the distal end of the second phalanx, and over the proximal end of the third phalanx.

Action.—Flexes digit IV.

Comparison.—No significant differences noted among the species studied.

Musculus flexor perforans et perforatus digiti II (Figs. 2, 9).—Small and spindle-shaped, this muscle lies on the posterolateral side of the crus immediately beneath the *pars externa* of the *m. gastrocnemius.* The origin is fleshy and arises in company with the *m. flexor perforans et perforatus digiti III* from a point on the posterolateral surface of the distal end of the femur between the point of origin of the *pars externa* of the *m. gastrocnemius* and the fibular condyle. The belly extends approximately one-fourth of the way down the crus and gives rise to the tendon of insertion which passes distally and superficially through the posterior edge of the tibial cartilage. The tendon traverses the posteromedial canal of the hypotarsus (Fig. 6) and continues along the posterior surface of the tarsometatarsus. Between the first metatarsal and the base of the second digit the tendon is enclosed by the medial surface of a sesamoid bone. This tendon then perforates that of the *m. flexor perforatus digiti II* at the level of the first phalanx and in turn is perforated by the tendon of the *m. flexor digitorum longus* at the proximal end of the second phalanx. The insertion is on the posterior surface of the second phalanx.

Action.—Flexes digit II.

Comparison. — In *Passer, Estrilda, Poephila, Hesperiphona, Carpodacus, Pinicola, Leucosticte, Spinus,* and *Loxia* the proximal portion of this muscle is more intimately connected with the posterior edge of the *m. flexor perforans et perforatus digiti III* than it is in the other species examined.

Musculus flexor perforans et perforatus digiti III (Fig. 2).—Long and pinnate, this muscle lies on the lateral surface of the crus beneath the *m. peroneus longus* and *pars externa* of the *m. gastrocnemius.* There are two distinct heads. The origin of the anterior head is fleshy from the proximal edge of the outer cnemial crest and from the internal edge of the distal end of the patellar tendon. The posterior head arises by a tendon from the femur in company with the *m. flexor perforans et perforatus digiti II,* is connected also with the tendon of origin of the *m. flexor perforatus digiti II,* and is loosely attached to the head of the fibula. Fibers from the belly of the muscle attach throughout its length to the lateral edge of the fibula, and the muscle is tightly fused also with adjacent muscles. The tendon of insertion is formed approximately one-half the way down the crus. The tendon perforates the posterior surface of the tibial cartilage and passes through the posteromedial canal of the hypotarsus (Fig. 6). At the base of the third digit the tendon ensheathes that of the *m. flexor digitorum longus* and the two together perforate the tendon of the *m. flexor perforatus digiti III.* Immediately distal to this perforation the tendon of the *m. flexor perforans et perforatus digiti III* ceases to ensheath that of the *m. flexor digitorum longus.* The latter passes beneath that of the former. Near the distal end of the second phalanx the tendon of the *m. flexor digitorum longus* perforates that of the *m. flexor perforans et perforatus digiti III.* The latter inserts on the posterior surface of the distal end of the second phalanx and the proximal end of the third.

Action.—Flexes digit III.

Comparison.—In *Passer, Estrilda,* and *Poephila,* and in all the cardueline finches examined the proximal portion of this muscle is more intimately connected with the anterior edge of the *m. flexor perforans et perforatus digiti II* than it is in the other species examined.

Musculus flexor digitorum longus (Figs. 3, 5).—This strong, pinnate muscle is deeply situated along the posterior surfaces of the tibia and fibula. There are two distinct heads of origin. The lateral head arises by means of fleshy fibers from the posterior edge of the head of the fibula. The medial head arises by means of fleshy fibers from the region under the ledgelike external and internal articular surfaces of the proximal end of the tibia. Neither head has any connection with the femur in contrast to the condition, described by Hudson (1937:46-47) in the crow, *Corvus brachyrhynchos,* and in the raven, *Corvus corax.* Near the point of insertion of the *m. biceps femoris* the two heads fuse. The common belly is attached by fleshy fibers to the posterior surface of the tibia and fibula for two-thirds of the distance down the crus. Near the distal end of the crus the muscle terminates in a strong tendon which passes deeply through the tibial cartilage and traverses the anteromedial canal of the hypotarsus (Fig. 6). About midway down the tarsometatarsus this tendon becomes ossified. Immediately above the bases of the toes it gives rise to three branches, one to the posterior surface of each of the foretoes. These branches perforate the other flexor muscles of the toes as described in the accounts of those muscles and insert as follows: The branch to digit II inserts on the base of the ungual phalanx and by a stout, tendinous slip on the distal end of the second phalanx (Fig. 9). The branch to digit III inserts on the base of the distal end of the third phalanx and a stronger slip to the distal end of the second or proximal end of the third. The branch to digit IV inserts on the base of the ungual phalanx, with one tendinous slip to the distal end of the third phalanx and another to the distal end of the fourth.

Action.—Flexes foretoes.

Comparison.—No significant differences noted among the species studied.

Musculus flexor hallucis longus (Fig. 3).—Situated immediately posterior to the *m. flexor digitorum longus,* the belly of this large, pinnate muscle is intimately connected anteriorly to that of the *m. flexor perforatus digiti II.* The *m. flexor hallucis longus* arises by two heads which are separated by the tendon of insertion of the *m. biceps femoris.* The smaller anterior head arises from the same tendon as does the *m. flexor perforatus digiti II*. The larger posterior head arises by means of fleshy fibers from the intercondyloid region of the posterior surface of the femur along with the *m. flexor perforatus digiti III* and *IV*. The two heads join just distal to the point of insertion of the *m. biceps femoris*. There is no trace of a tendinous band connecting the two heads as there is in the crow and in the raven (Hudson, 1937:49). Near the distal end of the shank the muscle gives rise to a strong tendon which perforates the tibial cartilage along its lateral edge and passes through the anterolateral canal of the hypotarsus (Fig. 6). The tendon crosses over to the medial surface of the tarsometatarsus, passes distally, and perforates the sheathlike tendon of the *m. flexor hallucis brevis* between the first metatarsal and the trochlea for digit II. The tendon continues along the posterior surface of the hallux and has a double insertion; the main tendon attaches to the base of the ungual phalanx and a smaller branch inserts on the distal end of the proximal phalanx.

Action.—Flexes hallux.

Comparison.—In *Vireo* this muscle has only the posterior head of origin and is not connected with the *m. flexor perforatus digiti II*. The muscle is proportionately smaller and weaker than in any of the other species studied.

Musculus extensor hallucis longus (Fig. 4).—One of the smallest muscles of the leg, the origin is fleshy from the anteromedial edge of the proximal end of the tarsometatarsus. The belly is long and slender and terminates distally in a slender tendon which passes distally along the posterior surfaces of the first metatarsal and the first digit. The insertion is on the base of the ungual phalanx. Near the distal end of the proximal phalanx, the tendon passes between two thick bands of fibro-elastic tissue which insert also on the ungual phalanx. These bands of tissue function as automatic extensors of the claw.

Action.—Extends hallux; action must be slight.

Comparison.—In *Vireo* this muscle is proportionately larger and better developed than it is in any of the other species examined.

Musculus flexor hallucis brevis (Fig. 4).—This minute muscle has a fleshy origin from the medial surface of the hypotarsus. The short belly terminates in a weak, slender tendon which passes down the posteromedial surface of the tarsometatarsus and into the space between the first metatarsal and the trochlea for digit II. In this region the tendon envelops the tendon of the *m. flexor hallucis longus* and inserts on the distal end of the first metatarsal and on the proximal end of the first phalanx of the first digit.

Action.—Flexes hallux; action must be slight.

Comparison.—The small size of this muscle makes it exceedingly difficult to study. The muscle is larger in *Vireo* than in any of the other species examined. This may be correlated with the smaller size of the *m. flexor hallucis longus* in this species. The muscle does not seem to be so well developed in the carduceline finches as it is in the other species.

Musculus abductor digiti IV (Fig. 2).—Extremely small, delicate and difficult to demonstrate, this muscle arises in a fleshy origin immediately from underneath the posterior edge of the external cotyla of the tarsometatarsus. The tendon of insertion is long and slender and inserts along the lateral edge of the first phalanx of digit IV.

Action.—Abducts digit IV.

Comparison.—No significant differences noted among the species studied.

Musculus lumbricalis.—Semitendinous throughout its length, this muscle arises from the ossified tendon of the *m. flexor digitorum longus* at a point immediately proximal to the branching of this tendon. The insertion is on the joint pulleys and capsules at the base of the third and fourth digits.

Action.—Hudson (1937:57) states that: "Meckel (*vide* Gadow—1891, p. 204) considered this muscle as serving to draw the joint pulley behind in order to protect it from pinching during the bending of the toes. It perhaps also tends to flex the third and fourth digits."

Comparison.—No significant differences noted among the species studied.

Discussion of the Myological Investigations

Simpson (1944:12) and others have emphasized that different parts of organisms evolve at different rates. Beecher (1951b:275) in stating that ". . . the hind limb is very similar in muscle pattern throughout the Order Passeriformes and seems to have become relatively static after attaining a high level of general efficiency . . ." implies that the muscle pattern of the leg must be one of long standing and slow change. This concept was emphasized by Hudson (1937) who found but little variation in muscle pattern among members of the several families of passerine birds. The concept is further confirmed by the present investigation. The intricate patterns of origin and of insertion seem to remain almost the same throughout the order in spite of adaptive radiation which has occurred.

Two major differences in patterns of leg-musculature, however, were found among the species studied, and these differences are significant since they are consistent between subfamilies. The muscles involved are the *m. obturator externus* and the *pars interna* of the *m. gastrocnemius.*

The *m. obturator externus* is bipartite, consisting of dorsal and ventral parts, in the passerine species studied by Hudson (1937) and in all of the species examined by me except the ploceids and the cardueline finches. In the ploceids and cardueline finches this muscle is undivided and resembles in its position, origin, and insertion only the ventral portion of the muscle found in the other birds studied. It is difficult to imagine what advantage or disadvantage might be associated with the bipartite or with the undivided condition. The action of this muscle is to rotate the femur (right femur clockwise, left femur counterclockwise), and certainly the greater mass of the bipartite muscle could lend greater strength to such action. The possible significance of this is discussed below.

List of Abbreviations Used in Figures

Abd. dig. IV	*M. abductor digiti IV*
Acc.	*M. accessorius semitendinosi*
Add. long.	*M. adductor longus et brevis*
Anterolat. can.	Anterolateral canal of hypotarsus
Anteromed. can.	Anteromedial canal of hypotarsus
Bic. fem.	*M. biceps femoris*
Bic. loop	Loop for *m. biceps femoris*
Ext. cot.	External cotyla
Ext. dig. l.	*M. extensor digitorum longus*
Ext. hal. l.	*M. extensor hallucis longus*
Fem. tib. ext.	*M. femorotibialis externus*
Fem. tib. int.	*M. femorotibialis internus*
Fem. tib med.	*M. femorotibialis medius*
F. dig l.	*M. flexor digitorum longus*
F. hal. brev.	*M. flexor hallucis brevis*
F. hal. l.	*M. flexor hallucis longus*
F. p. et p. d. II	*M. flexor perforans et perforatus digiti II*
F. p. et p. d. III	*M. flexor perforans et perforatus digiti III*
F. per. d. II	*M. flexor perforatus digiti II*
F. per. d. III	*M. flexor perforatus digiti III*
F. per. d. IV	*M. flexor perforatus digiti IV*
Gas.	*M. gastrocnemius*
Iliacus	*M. iliacus*
Il. tib.	*M. iliotibialis*
Il. troc. ant.	*M. iliotrochantericus anticus*
Il. troc. med.	*M. iliotrochantericus medius*
Il. troc. post.	*M. iliotrochantericus posticus*
Int. cot.	Internal cotyla
Isch. fem.	*M. ischiofemoralis*
Midmed. can.	Midmedial canal of hypotarsus
Obt. ext.	*M. obturator externus*
Obt. int.	*M. obturator internus*
P. ant.	*Pars anticus*
P. ext.	*Pars externa*
P. int.	*Pars interna*
P. med.	*Pars media*
P. post.	*Pars posticus*
Per. brev.	*M. peroneus brevis*
Per. long.	*M. peroneus longus*
Pirif.	*M. piriformis*
Plan.	*M. plantaris*
Posterolat. can.	Posterolateral canal of hypotarsus
Posteromed. can.	Posteromedial canal of hypotarsus
Sar.	*M. sartorius*
Semim.	*M. semimembranosus*
Semit.	*M. semitendinosus*
Tib. ant.	*M. tibialis anticus*
Tib. cart.	Tibial cartilage

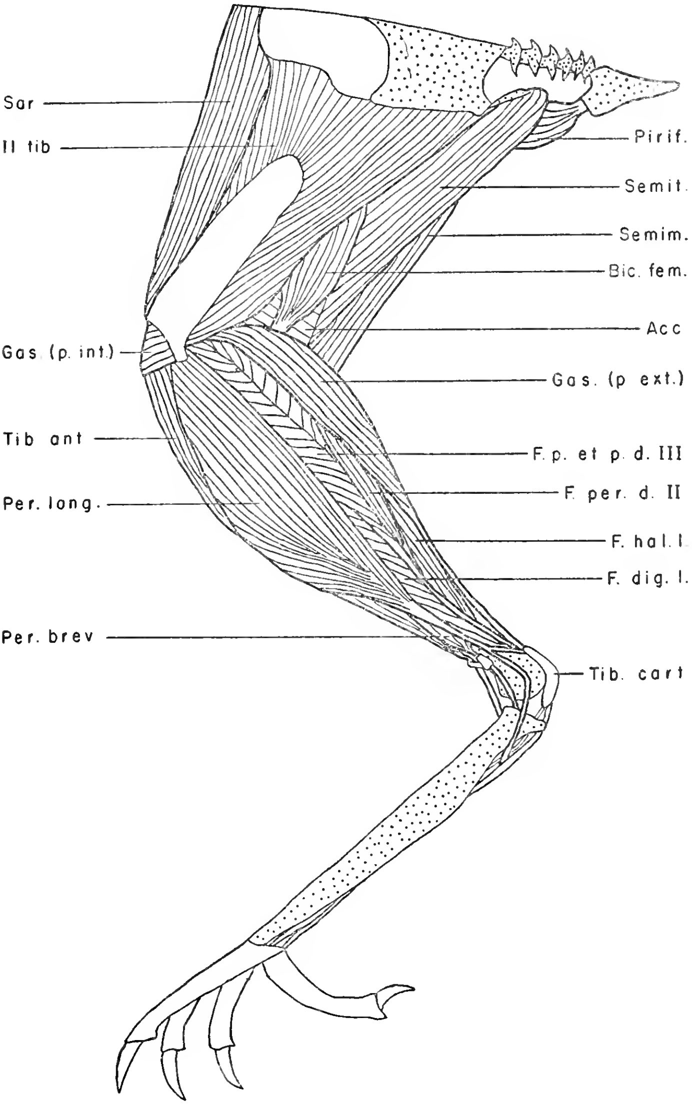


Fig. 1. *Pipilo erythrophthalmus.* Lateral view of the superficial muscles of the left leg, × 1.5.

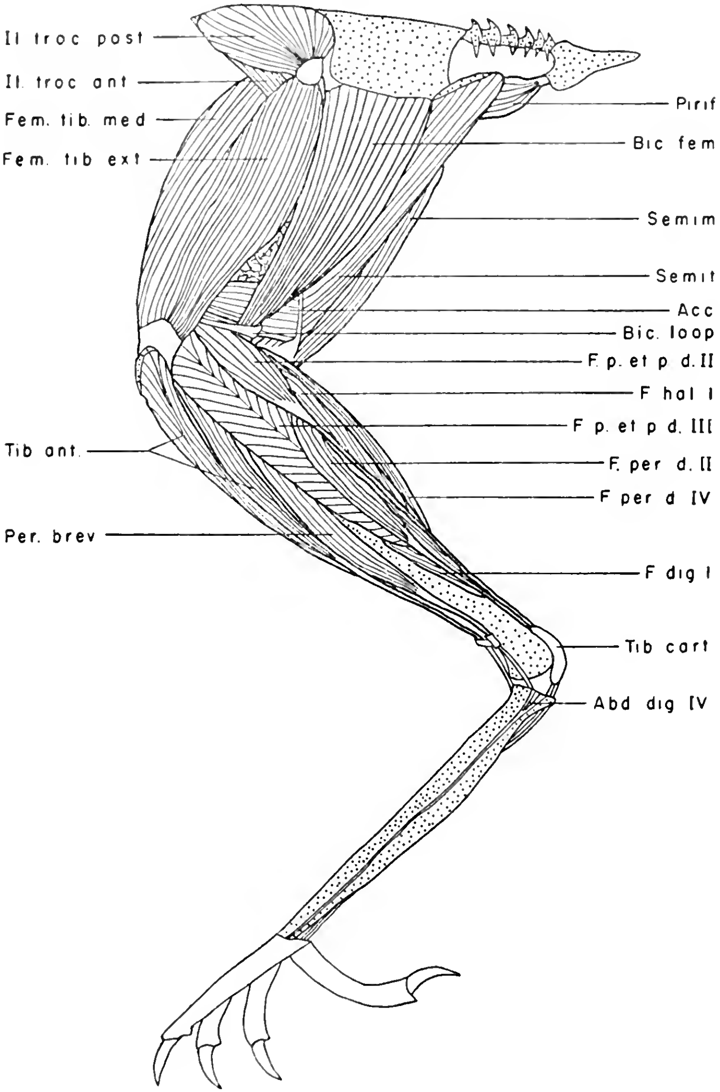


FIG. 2. *Pipilo erythrophthalmus.* Lateral view of the left leg showing a deeper set of muscles. The superficial muscles *iliotibialis, sartorius, gastrocnemius* and *peroneus longus* have been removed, × 1.5.

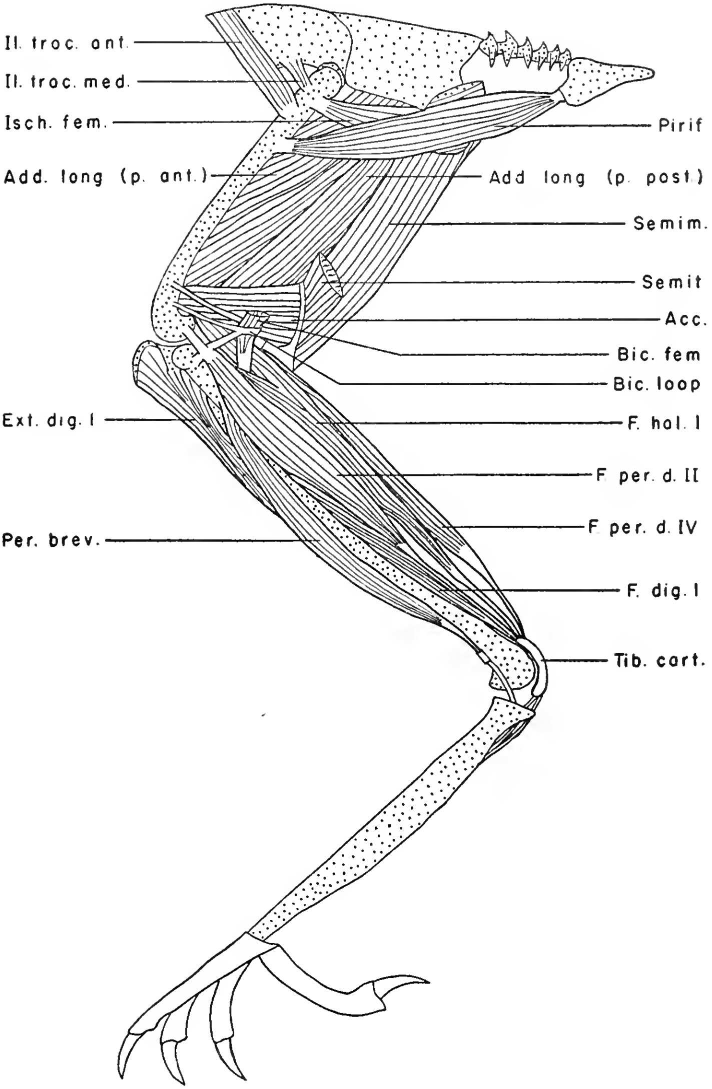


Fig. 3. *Pipilo erythrophthalmus.* Lateral view of the left leg showing the still deeper muscles. In addition to those listed for figure 2, the following muscles have been wholly or partly removed: *iliotrochantericus posticus, femorotibialis externus, femorotibialis medius, biceps femoris, semitendinosus, tibialis anticus, flexor perforans et perforatus digiti II,* and *flexor perforans et perforatus digiti III,* × 1.5.

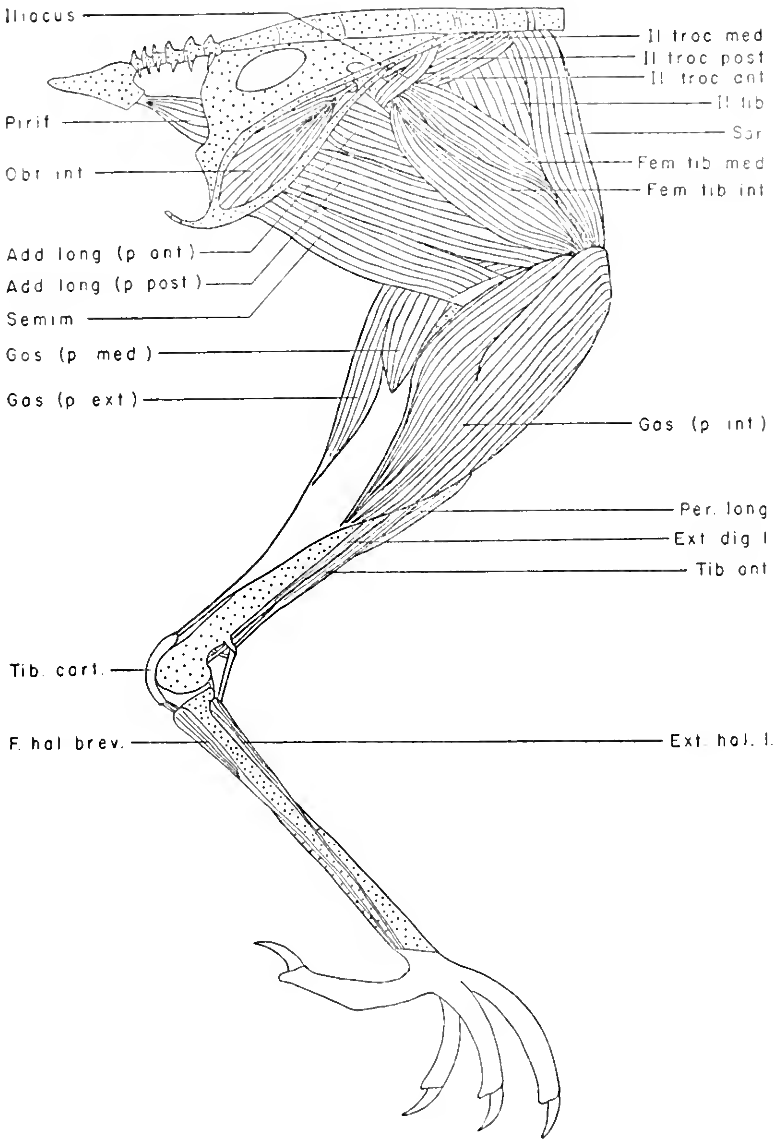


FIG. 4. *Pipilo erythrophthalmus.* Medial view of the superficial muscles of the left leg, × 1.5.

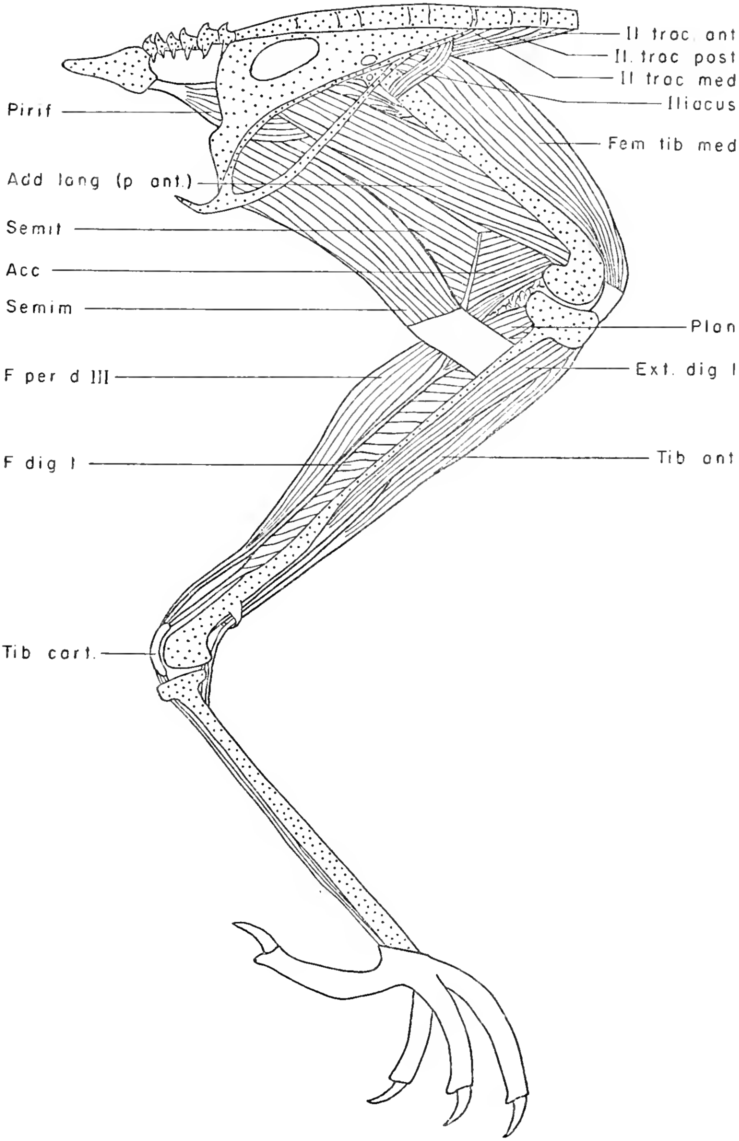


FIG. 5. *Pipilo erythrophthalmus.* Medial view of the left leg showing a deeper set of muscles than those seen in figure 4. The following superficial muscles have been removed: *iliotibialis, sartorius, femorotibialis internus, obturator internus, adductor longus (pars posticus), gastrocnemius,* and *peroneus longus,* × 1.5.

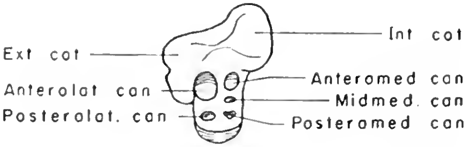


Figure 6

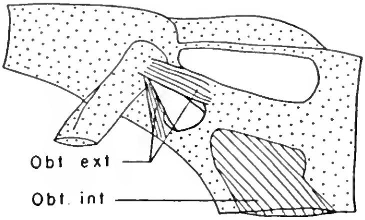


Figure 7

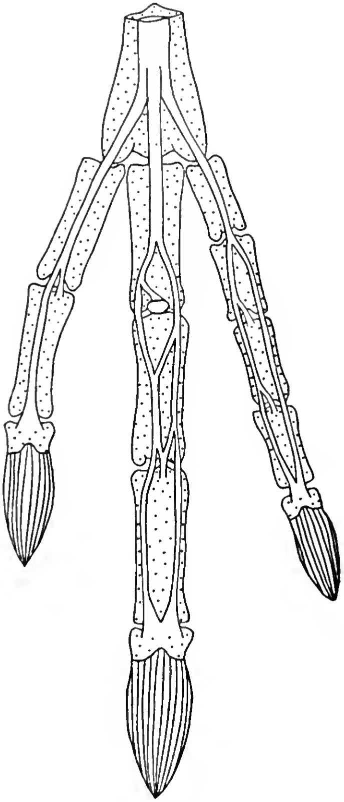


Figure 8

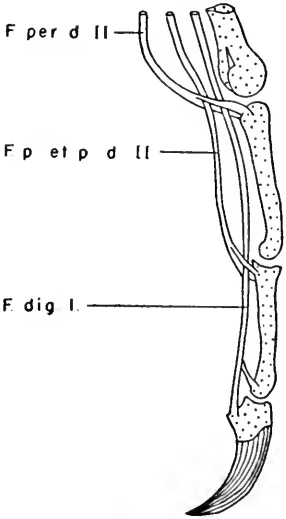


Figure 9

Fig. 6. *Pipilo erythrophthalmus.* Proximal end of left tarsometatarsus and the hypotarsus, × 4.

Fig. 7. *Pipilo erythrophthalmus.* Lateral view of proximal end of left femur and a portion of the pelvis, × 3.5.

Fig. 8. *Pipilo erythrophthalmus.* Upper surfaces of the phalanges of the foretoes of the left foot showing insertions of the *M. extensor digitorum longus,* × 3.

Fig. 9. *Pipilo erythrophthalmus.* Medial view of the second digit of the left foot, showing insertions of the flexor muscles, × 3.

The division of the *pars interna* of the *m. gastrocnemius* into anterior and posterior parts has not been reported by previous authors yet the division is quite distinct in those birds in which it occurs. Hudson (1937:36) points out that in some non-passerine birds the *pars interna* is double, but that in these species the *m. semimembranosus* inserts between the two parts. This is not the condition in those species studied by me. Only the ploceids and the cardueline finches in the present investigation fail to show such a division. The undivided muscle in these birds resembles, in its origin and position, the posterior portion of the muscle found in those species showing the bipartite condition. The greater mass of the bipartite muscle probably makes possible a stronger extension of the tarsometatarsus.

Thus, the divided or undivided conditions of the *m. obturator externus* and the *pars interna* of the *m. gastrocnemius* seem to be correlated with the degrees of strength of certain movements of the leg. It is conceivable that these differences in structure are correlated with the manner in which food is obtained, the birds having the bipartite muscles being those which spend the most time on the ground searching and scratching for seeds and other sorts of food. Yet, in *Leucosticte*, a cardueline, and in *Calcarius*, an emberizine, whose foraging habits are rather similar, the structure is unlike. *Leucosticte* does resemble the emberizines and also *Piranga* and *Spiza* in the extension of a band of muscle fibers from the *pars interna* of the *m. gastrocnemius* around the front of the knee. A band of muscle fibers of this sort strengthens the knee joint and gives still more strength to the *pars interna.* This condition has been reported in a number of birds by Hudson (1937) and is, in all probability, an adaptation for greater strength of certain leg movements. The development of this band in *Leucosticte* seems to parallel that in the other birds studied and does not indicate relationship, since in *Leucosticte* this band arises from the undivided muscle which (as stated above) resembles only the posterior portion of the bipartite muscle described for the other birds. In the latter. the muscular band arises from the anterior part of the muscle.

Minor differences in muscle pattern, like those already mentioned, are consistent also between subfamilies, but correlation of these minor differences with function is difficult. There is the implication, however, that in all the groups except the carduelines and ploceids, the emphasis is on greater strength and mobility of the leg. In the carduelines that were studied the origin of the *m. sartorius* does not extend so far craniad as in the other species. In the latter, at least half of the origin is from the last one or two free dorsal vertebrae; in the carduelines no more than one third of the origin is anterior to the ilium. It is conceivable that the more craniad the origin, the stronger the forward movement of the thigh would be.

In *Passer, Estrilda* and *Poephila,* and in all the cardueline finches examined, the bellies of the *m. flexor perforans et perforatus digiti II* and the *m. flexor perforans et perforatus digiti III* are more intimately connected than they are in the other species studied. Thus, the amount of independent action of these muscles in *Passer,* in the estrildines, and in the carduelines probably is reduced.

In *Passer,* the estrildines, and the carduelines the edges of the sheathlike tendon of insertion of the *m. perforatus digiti III* are thickened; as a result the insertion appears superficially to be double but closer examination reveals that there is a fascia stretched between the thickened edges. In the other species examined, the insertion is sheathlike throughout and there are no thick areas. I cannot explain this on the basis of function. The difference, however, is obvious and constant.

Aside from the differences noted above, there were variations of muscle pattern that seem to be significant only in *Vireo olivaceus.* In this species the central, aponeurotic portion of the *m. iliotibialis* is absent. The origin of the *m. adductor longus et brevis* is from the dorsal edge of the ischiopubic fenestra and not from the membrane covering this fenestra. The origin of the *pars posticus* of this muscle, furthermore, is fleshy and not tendinous as it is in the other species. The *m. flexor perforatus digiti II* is larger and more deeply situated in *Vireo* and has, furthermore, no connection with the *m. flexor hallucis longus.* The latter muscle is smaller and weaker than in any of the other species and has only one (the posterior) head of origin. The *m. flexor hallucis brevis,* on the contrary, is larger than in the other birds, compensating, probably, for the small *m. flexor hallucis longus.* In those differences, however, which separate the carduelines and ploceids from the other birds studied, *Vireo* resembles, in every instance, the richmondenines, emberizines, tanagers, warblers, and blackbirds.

On the basis of differences in leg-musculature the species which are now included in the Family Fringillidae may be separated into two groups. One group includes the richmondenines and the emberizines; the other, the carduelines. The muscle patterns of the legs of the birds of the first group are indistinguishable from those of *Seiurus, Icterus, Molothrus,* and *Piranga,* and except for the differences noted are similar to those in *Vireo*. The carduelines, on the other hand, are similar in every point of leg-musculature to the ploceids which were studied. Thus, the heterogeneity of the Family Fringillidae, as now recognized, is emphasized by differences in the muscle patterns of the leg.

COMPARATIVE SEROLOGY

General Statement

The application of serological techniques to the problems of animal relationships has been attempted with varying degrees of success over a period of approximately fifty years. Few of the earlier studies were of a quantitative nature, but within the past decade, satisfactory quantitative serological techniques have been developed whereby taxonomic relationships may be estimated. The usefulness of comparative serology in taxonomy has been demonstrated in investigations of many groups wherein results obtained have, in most instances, been compatible with the results obtained by more conventional methods, such as comparative morphology. As Boyden (1942:141) stated, "comparative serology . . . is no simple guide to animal relationship." However, the objectiveness of its methods, the fact that it has its basis in the comparisons of biochemical systems which seem to be relatively slow to change in response to external environmental influences, and the fact that the results are of quantitative nature favor, where possible, the inclusion of data from comparative serology along with that from more conventional sources when an attempt is made to determine the relationships of groups of animals.

The application of serological methods in ornithology has not been extensive. Irwin and Cole (1936) and Cumley and Irwin (1941, 1944) used two species of doves and their hybrids and demonstrated that a distinction between the red cells of these birds could be made by use of immunological methods involving the agglutinin reaction. McGibbon (1945) was able to distinguish the red cells of interspecific hybrids in ducks by similar methods. Irwin (1953) used similar techniques in his study of the evolutionary patterns of some antigenic substances of the blood cells of birds of the Family Columbidae. Sasaki (1928) demonstrated the usefulness of the precipitin technique in distinguishing species of ducks and their hybrids. This technique was used successfully also by DeFalco (1942) and by Martin and Leone (1952). Working with groups of known relationships, these investigators showed that the "accepted" systematic positions of certain birds were confirmed by serological procedures. The precipitin reaction, however, has never been applied to actual problems in avian taxonomy prior to the present study.

Preparation of Antigens

Although most previous work in comparative serology in which precipitin tests were used has involved the use of whole sera as antigens, Martin and Leone (1952) indicated that tissue extracts are satisfactory as antigens and that serological differentiation can be obtained with these extracts and the antisera to them. I decided, therefore, to use such extracts in these investigations, since the small sizes of the birds to be tested made it impracticable to obtain enough whole sera.

Most of the birds used were obtained by shooting, but a few were trapped and the exotic species were purchased alive from a pet dealer. When a bird was killed, the entire digestive tract was carefully removed to prevent the escape of digestive enzymes into the tissues and to prevent putrefaction by action of intestinal bacteria. As soon as possible (and within three hours in every instance) the bird was skinned, the head, wings, and legs were removed, and the body was frozen. Each specimen, consisting of trunk, heart, lungs, and kidneys, was wrapped separately and carefully in aluminum foil to prevent dehydration of the tissues. The specimens were kept frozen until the time when the extracts were made.

When an extract was to be prepared, the specimen was allowed to thaw but not to become warm. In the cold room with the temperature of all equipment and reagents at 2°C., the specimen was placed in a Waring blender with 0.9 per cent aqueous solution of NaCl buffered with M/150 K_2HPO_4 and M/150 Na_2HPO_4 to a pH of 7.0. The amount of reagent used was 75 ml. of saline for each gram of tissue to be extracted. The tissues were minced in the blender, allowed to stand at 2°C. for 72 hours, and the tissue residues removed by centrifugation in a refrigerated centrifuge. Formalin was added to a portion of the supernatant in the amount necessary to make the final dilution 0.4 per cent. This formolization was found to be necessary to inhibit the action of autolytic enzymes over the period of time required to complete the investigations. The effects of formolization on the antigenicity and reactivity of proteins are discussed later. It was necessary to sterilize and clarify the "native" (unformolized) extracts; this was done by filtration through a Seitz filter. These "native" substances were used only in the early stages of the investigation (see below). The filtrate was bottled and stored at 2°C. In the early stages of this investigation clarification of the formolized extract was accomplished by the same sort of filtration. It was determined, however, that centrifugation in a refrigerated centrifuge at high speeds (17,000g) served the same purpose and was quicker. The formolized extracts were bottled and also stored at 2°C. (although refrigerated storage of the formolized extracts does not seem necessary). For each extract the amount of protein present was determined colorimetrically by the method of Greenberg (1929) with a Leitz Photrometer.

Species for which extracts were prepared and the protein values of the extracts are listed in Table 1. Extracts of some species were used throughout most of the experiment; extracts of others were used only when needed for purposes of comparison.

Table 1.—Species from Which Extracts Were Prepared and Injection Schedules for Extracts Against Which Antisera Were Produced

Species	Protein, gms. per 100 ml.	Injection schedules for production of antisera
Myiarchus crinitus (Linnaeus)	0.65	Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml.
Passer domesticus	1.40	Series 1: Subcutaneous, 0.5, 1.0, 2.0, and 4.0 ml.
Estrilda amandava	0.45	*Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. *Series 2: Subcutaneous, 0.5, 1.0, and 2.0 ml. Intraperitoneal, 8.0 ml.
Poephila guttata	0.56	*Same as for *Estrilda*.
Molothrus ater	0.65	Series 1: Intavenous and subcutaneous, respectively, 0.5 and 0.5 ml., 1.0 and 1.0 ml., 3.0 and 1.0 ml., 5.0 and 3.0 ml. Series 2: Subcutaneous, 0.5, 1.0, 2.0 and 4.0 ml.
Piranga rubra	0.50	Same as for *Molothrus*.
Richmondena cardinalis	0.70	*Same as for *Estrilda*.
Richmondena cardinalis	0.60	Same as for *Spinus*.
Passerina cyanea	0.45	Antiserum not prepared.
Spiza americana	0.70	Same as for *Molothrus*.
Carpodacus purpureus	0.50	Antiserum not prepared.
Spinus tristis	0.49	Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. Series 2: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. Series 3: Subcutaneous, 0.5, 1.0, 2.0, and 4.0 ml.
Pipilo erythrophthalmus	0.92	Antiserum not prepared.
Junco hyemalis	0.56	Same as for *Spinus*.
Spizella arborea	0.48	Same as for *Spinus*.
Zonotrichia querula	0.48	Same as for *Spinus*.
Zonotrichia albicollis (Gmelin)	0.92	Antiserum not prepared.

* Antiserum prepared against formolized antigen.

Preparation of Antisera

All antisera were produced in rabbits (laboratory stock of *Oryctolagus cuniculus*). Three methods of injection of antigen were used in various combinations: intravenous, subcutaneous, and intraperitoneal. Injection schedules used in the production of each antiserum are listed in Table 1. Both formolized and "native" antigens were used. Each rabbit received one or more series of four injections, each injection being administered on alternate days and doubling in amount: 0.5 ml., 1.0 ml., 2.0 ml., and 4.0 ml. In all but two instances more than one series of injections was necessary to produce a useful antiserum. More than two series, however, resulted in little or no improvement of the reactivity of the antiserum.

The injection-series were separated by intervals of eight days. On the eighth day after the last injection of each series, 10 ml. of blood were withdrawn from the main artery of the ear of the rabbit, and the antiserum was used in a homologous precipitin test to determine its usefulness. If the antiserum contained sufficient amounts of antibodies to conduct the projected tests, the rabbit was completely exsanguinated by cardiac puncture, by using an 18-gauge needle and a 50 ml. syringe. The whole blood was placed in clean test tubes and allowed to clot. It was allowed to stand at 2°C. for 12 to 18 hours so that most of the serum would be expressed from the clot. The serum was then decanted, centrifuged to remove all blood cells, sterilized in a Seitz filter, bottled in sterile vials, and stored at 2°C. until used.

Methods of Serological Testing

The precipitin reaction is the most successful of the serological techniques thus far devised for systematic comparisons. The reaction occurs because antigenic substances introduced into the body of an animal cause the formation of antibodies which precipitate antigens when the two are mixed. The antisera which are produced show quantitative specificities in their actions; therefore, when an antiserum containing precipitins is mixed with each of several antigens, the reaction involving the homologous antigen (that used in the production of the antiserum) is greater than those reactions involving the heterologous antigens (antigens other than those used in the production of the antiserum). Furthermore, the magnitudes of the reactions between the antiserum and the heterologous antigens vary according to the degrees of similarity of these antigens to the homologous one.

The method of precipitin testing follows that outlined by Leone (1949). The Libby (1938) Photronreflectometer was used to measure the turbidities developed by the interaction of antigen and antiserum. With this instrument parallel rays of light are passed through the turbid systems being measured. Light rays are reflected from the suspended particles to the sensitive plate of a photoelectric cell; this generates a current of electricity which causes a deflection on a galvanometer. The deflection is proportional to the amount of turbidity developed and readings may be taken directly from the scale of the instrument.

The reaction-cells of the photronreflectometer are designed to operate with a volume of 2 ml.; therefore, this volume was used in all testing. In every series of tests the amount of antiserum was held constant and the amount of antigen was varied. The volume for each antigen dilution was always 1.7 ml., and to this was added 0.3 ml. of antiserum to make up a volume of 2 ml.

Antigens were diluted with 0.9 per cent phosphate-buffered saline solution. Tests were run in standard Kolmer test-tube racks, each test consisting of 12 tubes. Each dilution was made on the basis of the known protein concentration of the antigen. The first tube contained an initial dilution of 1 part protein in 250 parts saline and each successive tube contained a protein dilution one-half the concentration of the preceding tube, ranging up to 1:512,000. Saline controls, antiserum controls, and antigen controls were maintained with each test to determine the turbidities inherent in these solutions. These control-turbidities were deducted from the total turbidity developed in each reaction-tube, the resultant turbidity then being considered as that which was caused by the interaction of antigens and antibodies. The turbidities were allowed to develop over a 24-hour period. In the early stages of this investigation the reactions were allowed to take place at 2°C. in order to inhibit bacterial growth.

TABLE 2.—Percentage values obtained from analyses of precipitin reactions. Numerals represent relative amounts of reaction between antigens and antisera. Homologous reactions are arbitrarily valued as 100 per cent, and heterologous reactions are expressed accordingly. *Comparisons are meaningful only if made within each horizontal row of values.*

ANTIGENS	ANTISERA							
	Estrilda amandava	*Poephila guttata*	*Piranga rubra*	*Richmondena cardinalis*	*Spiza americana*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
Passer domesticus	75	74	73	66	81	72	.....	81
Estrilda amandava	100	88	75	.....	79	72	53	.....
Poephila guttata	95	100	77	67	87	81	.....	.....
Molothrus ater	66	54	69	65	86	75	69	75
Piranga rubra	.....	.....	100	.....	.....	.....	.....	89
Richmondena cardinalis	75	80	91	100	98	65	88	91
Spiza americana	65	68	.....	71	100	64	67	80
Carpodacus purpureus	70	71	71	61	89	93	53	70
Spinus tristis	72	74	73	60	89	100	60	.....
Junco hyemalis	64	56	74	65	87	68	100	.....
Zonotrichia querula	65	71	.....	67	89	75	.....	100

Later tests were carried out at room temperatures, and bacterial growth was prevented by the addition to each tube of 'Merthiolate' in a final dilution of 1:10,000.

Experimental Data

Corrected values for the turbidities obtained were plotted with the turbidity values on the ordinate and the antigen dilutions on the abscissa. The homologous reaction was the standard of reference for all other test reactions with the same antiserum. By summing the plotted turbidity readings, numerical values are obtained which are indices serving to characterize the curves. Such values were converted to percentage values, that of the homologous reaction being considered 100 per cent. These values, plus the curves, provide the data by means of which the proteins of the birds may be compared. Plots representative of the precipitin curves are presented in Figs. 10 to 21. For convenience each plot represents only several of the 10 curves obtained with each antiserum.

A summary of the serological relationships of the birds involved in the precipitin tests is presented in Table 2, in which percentage values are presented. Since the techniques involved in testing were greatly improved as the investigation proceeded, the summary is based solely on those tests run in the later stages of the investigation. For reasons which will become apparent in later discussion, it should be emphasized that in Table 2 comparisons may be made only within each horizontal row of values.

Discussion of the Serological Investigations

One of the problems met early in this investigation was instability of the proteins in the extracts that were prepared. Extracts in which no attempt was made to inactivate the enzymes present proved unsatisfactory. It was necessary to maintain the temperature of the "native" antigens at 2°C., and all work with such antigens had to be performed at this temperature. This arrangement was inconvenient; furthermore, inactivation of the enzymes was not complete even at this low temperature, and some denaturation of the proteins took place as evidenced by the gradual appearance of insoluble precipitates in the stored vials.

The preservatives, 'Merthiolate' and formalin, were used in an attempt to inhibit the autolytic action of the enzymes present. Formalin, when added to make a final dilution of 0.4 per cent, proved to be the more satisfactory of the two preservatives and was used throughout most of the work. Formalin caused slight denaturation of some of the proteins, but this effect was complete within a few hours, after which any denatured material was removed by filtration or centrifugation. The proteins remaining in solution were stable over the period necessary to complete the investigations.

The addition of formalin reduces the reactivity of the extracts when they are tested with antisera prepared against "native" antigens and causes changes in the nature of the precipitin curves. This effect has been pointed out by Horsfall (1934) and by Leone (1953) in their work on the effects of formaldehyde on serum proteins. Their data indicate, however, that even though changes in the immunological characteristics of proteins are brought about by formolization, the proteins retain enough of their specific chemical characteristics to allow consistent differentiation of species by immunological methods. In the tests which I performed, the relative positions of the precipitin curves, whether native or formolized extracts were involved, remained unchanged (Figs. 10, 11). *All data used in interpretation of the serological relationships were obtained from tests in which formolized antigens of equivalent age were used.*

Only three antisera were produced against formolized antigens, all others being produced against "native" extracts. The formolized antigens seemed to have a greater antigenicity, in most instances, than did those which were unformolized, and precipitin reactions involving antisera produced against formolized antigens developed higher turbidities. The antisera produced against formolized antigens were equal to but no better than those prepared against "native" extracts in separating the birds tested (Figs. 12, 13).

The rabbit is a variable to be considered in serological tests. Two rabbits exposed to the same antigen, under the same conditions, may produce antisera which differ greatly in their capacities to distinguish different antigens. It is logical to assume, therefore, that two rabbits exposed to different antigens may produce antisera which also differ in this respect. This explains the unequal values of reciprocal tests shown in Table 2. Thus, in the test involving the antiserum to the extracts of *Richmondena*, a value of 71 per cent was obtained for *Spiza* antigen, whereas in the test involving anti-*Spiza* serum, a value of 98 per cent was obtained for *Richmondena* antigen. In Table 2, therefore, comparisons may be made only among values for the proteins of birds tested with the same antiserum.

Since the amount of any one antiserum is limited, there is, of necessity, a limit as to the number of birds used in a series of serological tests. Therefore, although the results reveal the actual serological relationships of the individual species, interpretation of the relationships of the taxonomic groups must be undertaken with the realization that such an interpretation is based on tests involving relatively few species of each group. It is reasonable to assume, however, that a species which has been placed in a group on the basis of resemblances other than serological resemblance would show greater serological correspondence to other members of that group than it would to members of other groups. Specifically, in the Fringillidae and their allies, there seems to be little reason to doubt that genera, and even subfamilies, are natural groups. This is illustrated in tests involving closely related genera: *Richmondena* and *Spiza* (Figs. 14, 15, 18), *Estrilda* and *Poephila* (Fig. 21), *Spinus* and *Carpodacus* (Figs. 12, 17, 19, 20). In each of these tests the pairs of genera mentioned show greater serological correspondence to each other than they do to other kinds involved. This point is illustrated further by a test (not illustrated) involving *Zonotrichia querula* (the homologous antigen) and *Zonotrichia albicollis.* Although this test was one of an earlier series in which difficulties were encountered (the data, therefore, were not used), it is of interest that the two species were almost indistinguishable serologically.

The serological homogeneity of passeriform birds is emphasized by the fact that the value of every heterologous reaction was more than 50 per cent of the value of the homologous reaction, except in the test involving the anti-*Richmondena* serum and *Myiarchus* (Fig. 13) in which the value of the heterologous reaction was 45 per cent. Because most ornithologists consider these genera to be only distantly related (they are in different suborders within the Order Passeriformes), the relatively high value of the heterologous reaction emphasizes the close serological correspondence of passerine birds and indicates that small consistent serological differences among these birds are actually significant. The possibility that some of the serological correspondence is due to the "homologizing" effect of formalin on proteins should not be excluded. I think, however, that this effect is not entirely responsible for the close correspondence observed here.

An additional point to consider in interpretation of the serological tests is that the techniques used tend to separate sharply species that are closely related whereas species that are distantly related are not so easily separated. In other words, comparative serological studies with the photronreflectometer tend to minimize the differences between distant relatives and to exaggerate the differences between close relatives.

In analyzing the serological relationships of the species used in this study, it becomes obvious that two or more series of tests must be considered before the birds can be placed in relation to each other. For example, the data presented in Fig. 14 indicate that *Spiza* and *Molothrus* show approximately the same degree of serological correspondence to *Richmondena.* This does not imply necessarily that *Spiza* and *Molothrus* are closely related. If Fig. 15 is examined, it can be determined that *Richmondena* shows much greater serological correspondence to *Spiza* than does *Molothrus*. Thus, an analysis of both figures serves to clarify the true serological relationships of the three genera. By reference to other series of tests involving these three birds a more exact determination of their relationships may be obtained.

To illustrate this point by a hypothetical example, two species might seem equidistant, serologically, from a third species. Additional testing should indicate if the first two species are equidistant in the same direction (therefore, by implication, close relatives) or in opposite directions (therefore, distant relatives). A single test supplies only two dimensions of a three dimensional arrangement.

It is impossible to interpret and to picture the serological data satisfactorily in two dimensions; therefore, a three-dimensional model (Figs. 22, 23) was constructed to summarize the serological relationships of the birds involved. Each of the eleven kinds used consistently throughout the investigation is represented in the model. By use of the percentage values (Table 2), each bird was located in relation to the other birds. Where possible, averages of reciprocal tests (Table 3) were used in determining distances between the elements of the model. In this way seven of the birds were accurately located in relation to each other. Lacking reciprocal tests, the positions of the other birds were determined by the values of single tests (Table 4). Although these birds were placed with less certainty, at least four points of reference were used in locating each species. At least one serological test is represented by each connecting bar in the model. The lengths of the bars connecting any two elements were determined as follows: a percentage value (Table 3 and Table 4) representing the degree of serological correspondence between two birds was subtracted from 100 per cent; the remainder was multiplied by a factor of five to increase the size of the model and the product was expressed in millimeters; a bar of proper length connects the two elements involved.

From the model it is observed that, *Molothrus* and *Passer* excluded, the birds fall into two distinct groups: one includes *Piranga, Richmondena, Spiza, Junco,* and *Zonotrichia;* the other includes *Estrilda, Poephila, Carpodacus,* and *Spinus.*

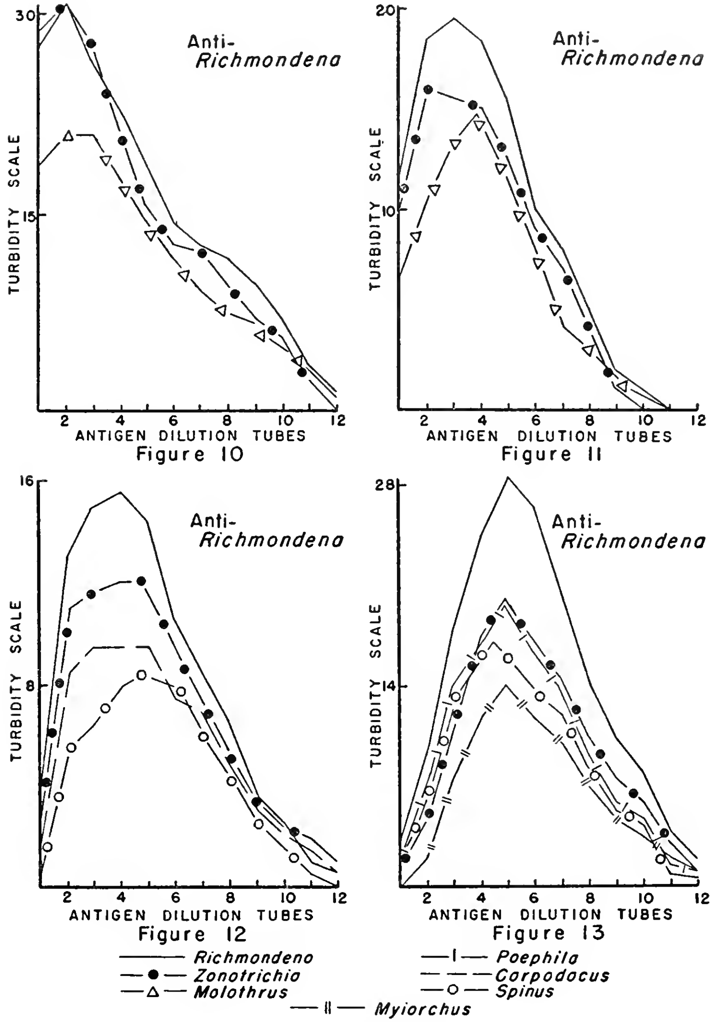
Within the richmondenine-emberizine-thraupid assemblage, *Junco* and *Zonotrichia* constitute a sub-group apart from the others. *Piranga* and *Richmondena* show close serological correspondence. The present taxonomic position of *Spiza* in the Richmondeninae,

TABLE 3.—RECIPROCAL VALUES USED TO DETERMINE DISTANCES BETWEEN ELEMENTS OF THE MODEL; EACH VALUE REPRESENTS THE AVERAGE OF SEROLOGICAL TESTS BETWEEN THE SPECIES INVOLVED

	Estrilda amandava	*Poephila guttata*	*Richmondena cardinalis*	*Spiza americana*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
Estrilda amandava	......	92	......	72	72	59	......
Poephila guttata	92	......	74	78	78	......	......
Richmondena cardinalis	......	74	......	85	63	77	79
Spiza americana	72	78	85	......	77	77	85
Spinus tristis	72	78	63	77	......	......	......
Junco hyemalis	......	......	77	77	......	......	......
Zonotrichia querula	......	......	79	85	......	......	......

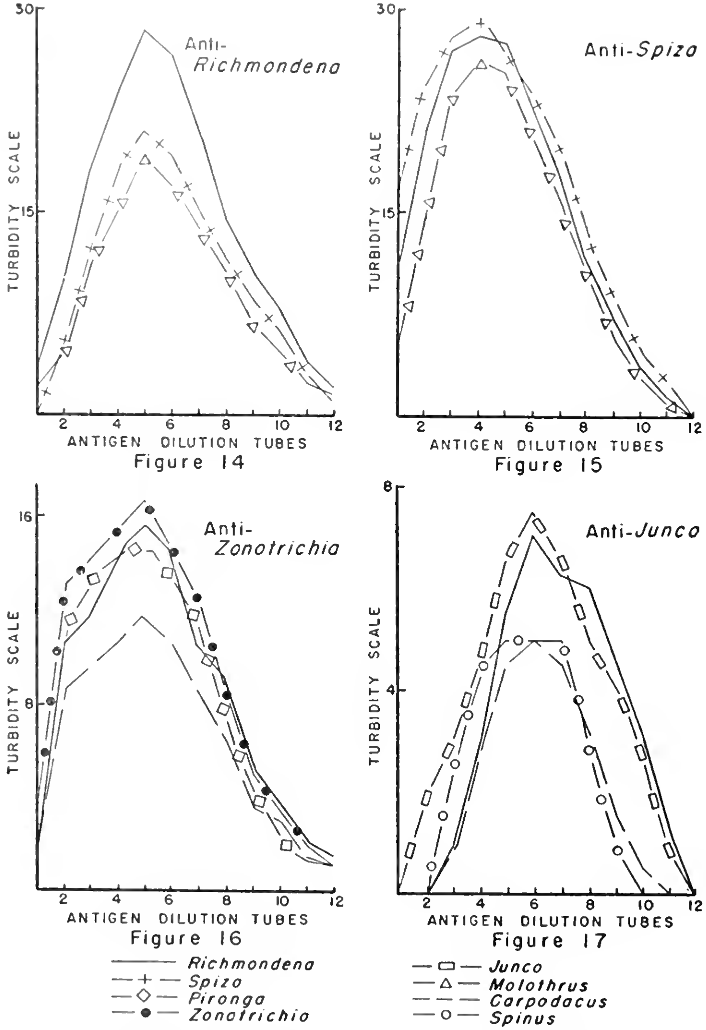
TABLE 4.—SINGLE VALUES USED TO DETERMINE DISTANCES BETWEEN ELEMENTS OF THE MODEL; EACH VALUE REPRESENTS A SINGLE TEST BETWEEN THE SPECIES INVOLVED

	Estrilda amandava	*Poephila guttata*	*Piranga rubra*	*Richmondena cardinalis*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
Passer domesticus	......	71	73	......	72	......	......
Molothrus ater	......	54	......	65	......	69	75
Piranga rubra	......	77	......	91	73	74	......
Carpodacus purpureus	70	71	......	61	93	......	......



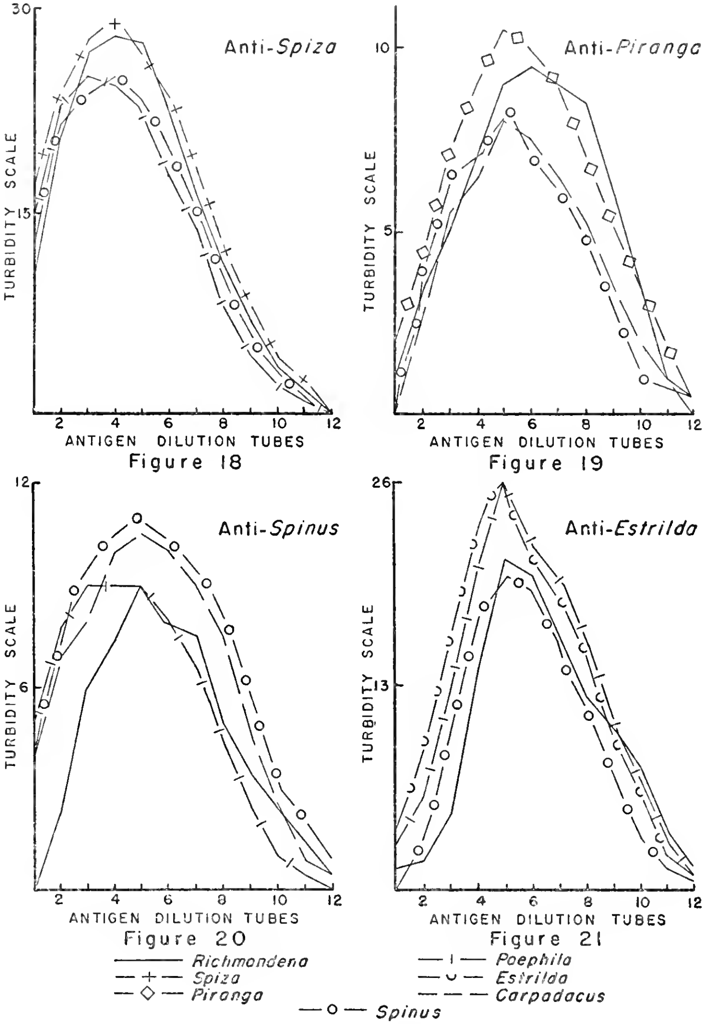
Figs. 10-13. Graphs of precipitin reactions illustrating effects of formalin on antigenicity and reactivity of the extracts. For further information, see text, pp. 190-193.

Fig. 10. Reactions of unformolized antigens of *Richmondena, Zonotrichia,* and *Molothrus* with anti-*Richmondena* serum. Fig. 11. Reactions of formolized antigens of *Richmondena, Zonotrichia,* and *Molothrus* with anti-*Richmondena* serum. Fig. 12. Reactions of anti-*Richmondena* serum prepared against native antigen with antigens of *Richmondena, Zonotrichia, Carpodacus,* and *Spinus.* Fig. 13. Reactions of anti-*Richmondena* serum prepared against formolized antigen with antigens of *Richmondena, Zonotrichia, Poephila, Spinus,* and *Myiarchus.*



Figs. 14-17. Graphs of precipitin reactions illustrating serological relationships. For further explanation, see text, pp. 190-193.

Fig. 14. Serological relationships of *Richmondena, Spiza,* and ***Molothrus.*** Fig. 15. Serological relationships of *Richmondena, Spiza,* and ***Molothrus.*** Fig. 16. Serological relationships of *Carpodacus* with the richmondenine-emberizine-thraupid assemblage. Fig. 17. Serological relationships of ***Carpodacus*** and *Spinus* with *Richmondena* and *Junco.*



FIGS. 18-21. Graphs of precipitin reactions illustrating serological relationships. For further explanation, see text, pp. 190-193.

FIG. 18. Serological relationships of *Spinus* and *Poephila* with the richmondenines. FIG. 19. Serological relationships of *Carpodacus* and *Spinus* with *Richmondena* and *Piranga*. FIG. 20. Serological relationships of *Poephila* and *Richmondena* with the carduelines. FIG. 21. Serological relationships of *Richmondena* and *Spinus* with the estrildines.

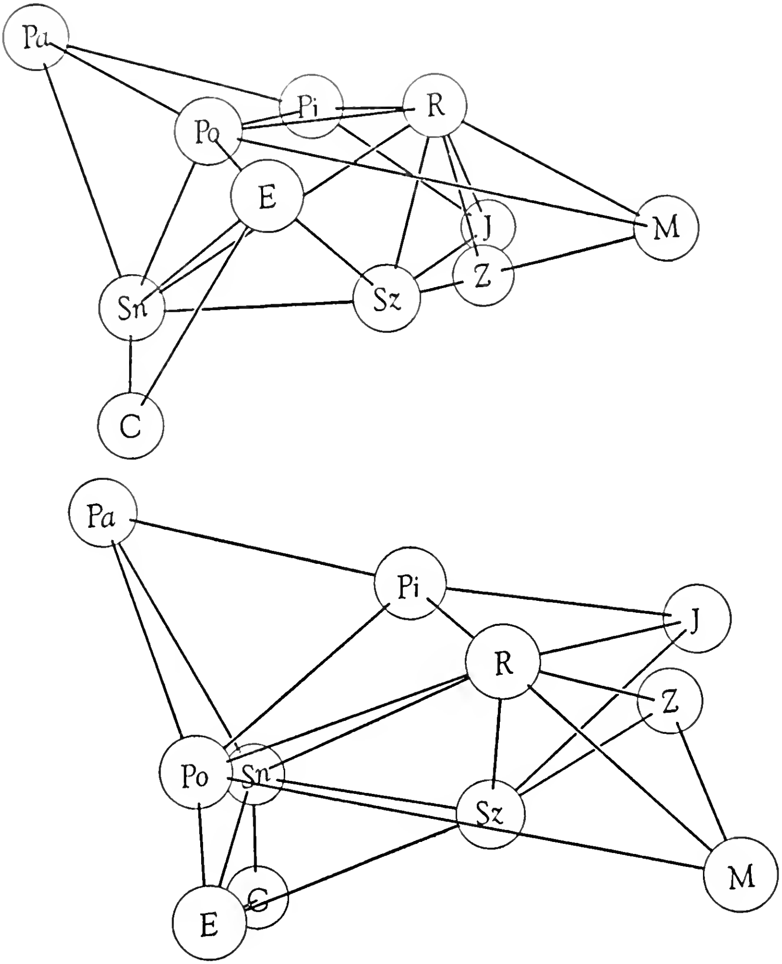


FIG. 22. Two views of a model illustrating serological relationships among fringillid and related birds. For further explanation, see text, pp. 193-194.

Genera			
C	*Carpodacus*	Pi	*Piranga*
E	*Estrilda*	Po	*Poephila*
J	*Junco*	R	*Richmondena*
M	*Molothrus*	Sn	*Spinus*
Pa	*Passer*	Sz	*Spiza*
		Z	*Zonotrichia*

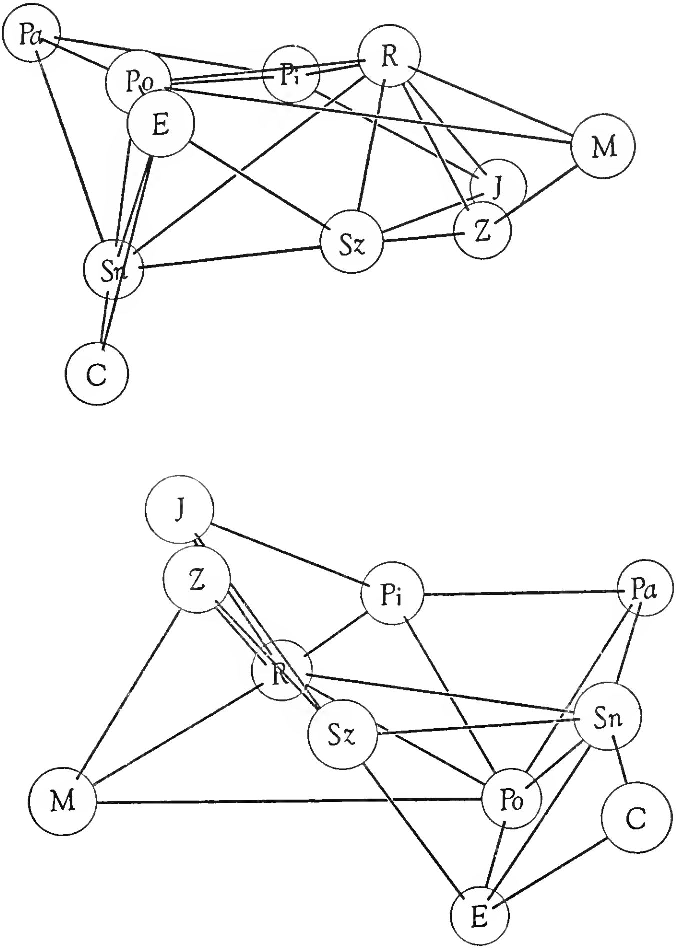


FIG. 23. Two additional views of the model shown in fig. 22 illustrating serological relationships among fringillid and related birds. For further explanation, see text, pp. 193-194.

Genera

C	*Carpodacus*
E	*Estrilda*
J	*Junco*
M	*Molothrus*
Pa	*Passer*
Pi	*Piranga*
Po	*Poephila*
R	*Richmondena*
Sn	*Spinus*
Sz	*Spiza*
Z	*Zonotrichia*

which has been questioned by Beecher (1951a:431; 1953:309), is corroborated at least insofar as the serological evidence is concerned. Certainly, serological correspondence of *Spiza* with the richmondenine-emberizine-thraupid assemblage is greater than with any other group of birds tested.

It is obvious that the serological affinities of the carduelines do not lie with the richmondenines, emberizines, or thraupids. The carduelines show greater serological correspondence with the estrildines than they do with any of the other groups tested. Further serological investigation involving other species, however, is necessary before the nearest relatives of the carduelines can be determined with certainty.

The two estrildines tested (*Estrilda* and *Poephila*) show close serological relationship. Their nearest relatives, serologically, seem to be the carduelines. The classification (Wetmore, 1951) that places *Passer* in the same family with the estrildines is not upheld by the serological data available. *Passer* is not, serologically, closely related to any of the birds tested. It is of interest that Beecher (1953:303-305), on the basis of jaw musculature, places *Passer* and the estrildines in separate families (Ploceidae and Estrildidae, respectively).

Molothrus shows greater serological correspondence to the richmondenine-emberizine-thraupid assemblage than to any of the other birds tested. It is definitely set apart from this group, however, and its position, serologically, is compatible with that based on evidence from other sources.

There seems to be but little argument among ornithologists that icterids, fringillids, and ploceids constitute families which are distinct from one another. If, then, the serological differences between *Molothrus* (Icteridae) and *Richmondena* (Fringillidae), between *Molothrus* and *Zonotrichia* (Fringillidae), and between *Richmondena* and *Poephila* (Ploceidae) are indicative of family differences, there are four families represented by the birds involved. *Molothrus* represents one family; *Piranga, Richmondena, Spiza, Junco,* and *Zonotrichia,* a second; *Estrilda, Poephila, Carpodacus,* and *Spinus,* a third; and *Passer,* a fourth.

CONCLUSIONS

The heterogeneity of the Family Fringillidae has been emphasized by many authors. The relationships of the species now included in this Family have been the subject of much discussion and constitute an important problem in avian systematics.

Sushkin's studies (1924, 1925) of features of the horny and bony palates have served as a basis for the present division of the Family into subfamilies. Recently, Beecher (1951a, 1951b, 1953) and Tordoff (1954) have used these features and others which they thought to be of value in an attempt to clarify the relationships of the species involved.

Beecher's work (1951a, 1951b, 1953) on jaw-musculature is a valuable contribution to our knowledge of the anatomy of passerine birds. His myological studies were so thorough and his presentation so detailed that students who disagree with his interpretations can draw their own conclusions. Beecher (1951b:276) points out that there are two basic types of skeletal muscle—those with parallel fibers and those with pinnately arranged fibers. The muscles with pinnate fibers seem to be more efficient, each muscle having a greater functional cross section for its bulk than does one with parallel fibers. He assumes that muscles with parallel fibers are more primitive, phylogenetically, than are those with fibers arranged pinnately. Since his study of the jaw muscles of the Icteridae (1951a) revealed that patterns of jaw-musculature within this Family remain constant regardless of the methods used in procuring food, he assumes that such patterns may be used as indicators of relationship throughout the entire oscinine group. These two assumptions, then, serve as the basis for his hypothesis concerning relationship and phylogeny within this assemblage. Beecher (1951b:278-280; 1953:310-312) maintains that within the Family Thraupidae there are two main lines which lead with almost no disjunction to the Carduelinae and Richmondeninae. The thraupid-richmondenine line involves a shift in the nature of the *m. adductor mandibulae externus superficialis,* which becomes more pinnate in the richmondenines. This results in greater crushing power. The thraupid-cardueline line involves a shift in emphasis from the *m. adductor mandibulae externus medialis* to the *m. pseudotemporalis superficialis* and the forward advance of the insertion of the latter. This, also, promotes greater crushing ability. He states that features of the horny palate and of the plumage provide further evidence of close relationship of these groups. He includes, therefore, the

Thraupinae, the Carduelinae, and the Pyrrhuloxiinae (=Richmondeninae) in the Family Thraupidae. Beecher (1953:307) indicates that the patterns of jaw-musculature of the Parulinae (wood warblers) and Emberizinae (buntings) are similar and suggests that the buntings had their origin from the wood warblers. He includes these subfamilies, therefore, in the Family Parulidae.

Beecher's reasoning may be criticized on several points. It may be, as he suggests, that muscles with parallel fibers evolved earlier, phylogenetically, than did muscles with pinnate fibers, but he does not give adequate consideration, it seems to me, to the possibility that parallel fibers may also have evolved secondarily from pinnate fibers. Since Beecher (1951a) found that patterns of jaw-musculature within the Family Icteridae were conservative, he is reluctant to admit the possibility of convergence among any of the other families. Differences in patterns of jaw-musculature are, however, functional adaptations and like the bill, which is also associated with food-getting may be subject to rapid evolutionary change. Finally, in attempting to classify the oscines, he has relied almost entirely on a single character—the pattern of jaw-musculature.

Tordoff's attempts (1954) to clarify the relationships of the fringillids and related species are based chiefly on features of the bony palate. He assumes that since palato-maxillaries seem to be absent in the majority of passerine birds, their occurrence in certain nine-primaried oscine groups indicates relationship among these groups. He points out that these bones, when present, are important areas of origin of the *m. pterygoideus* which functions in depression of the upper jaw and in elevation of the lower jaw. He assumes, therefore, that palato-maxillaries were evolved to provide for a more effective action of the *m. pterygoideus.* The need for such action could be associated with a seed-eating habit. All richmondenines and emberizines possess palato-maxillary bones either free or fused to the prepalatine bar, but there is no trace of these bones in the carduelines. Carduelines, furthermore, possess prepalatine bars that are characteristically flared anteriorly. This condition does not exist in the richmondenines or in the emberizines.

Tordoff points out, also, that the irregular, erratic migrations of the New World Carduelinae are unlike the more regular migrations of the richmondenines and emberizines. The carduelines, furthermore, are more arboreal in their habits than are these other groups and exhibit a decided lack of nest sanitation during the later stages of nesting, a situation which contrasts with that found in the Richmondeninae and Emberizinae. He suggests, therefore, that the carduelines are not so closely related to the richmondenines and the emberizines as previously has been thought.

Since there are only two cardueline genera, *Loximitris* and *Hesperiphona,* endemic to the New World and at least 10 genera with many species endemic to the Old World, Tordoff (1954:15) suggests an Old World origin for the carduelines. He strengthens his argument for this hypothesis by pointing out that in features of the bony palate and in habits the carduelines resemble the estrildines of the Family Ploceidae.

Tordoff (1954:29-30) states that the tanagers not only merge with the richmondenines but also grade imperceptibly into the emberizines. He includes, therefore, the Richmondeninae, Emberizinae, and Thraupinae in the Family Fringillidae. He suggests that the carduelines are ploceids, closely related to the Subfamily Estrildinae, on the basis of structure of the bony palate, geographic distribution, social behavior, and habits such as nest-fouling and nest-building.

Tordoff, like Beecher, has based his interpretations chiefly on one feature—structure of the bony palate. Since this feature also is associated with food-getting, the possibilities of convergence of distantly related species with similar habits and divergence of closely related species with different habits may not be excluded.

The hazard of unrecognized adaptive convergence cannot, of course, be excluded from most fields of taxonomic research, but some features of morphology and biochemistry are notably more conservative than others and undergo slower evolutionary change. Such features are often of utmost importance in distinguishing the higher taxonomic categories.

Most ornithologists are aware that, within the Order Passeriformes, patterns of musculature in the leg have evolved at a slow rate and exhibit little variation within the Order. Differences which do occur, therefore, probably are significant, especially those that are consistent between groups of species. As I have pointed out earlier (p. 184), there are no significant differences in leg-musculature between the Richmondeninae, Emberizinae, and Thraupidae. Indeed, it is difficult to define these groups on the basis of leg-musculature. If these groups are of common origin, the lack of distinct boundaries between them is not surprising. A muscular band which extends from the *pars interna* of the *m. gastrocnemius* around the front of the knee is present in every emberizine species that I studied and in the Genus *Piranga.* With the exception of *Spiza* none of the richmondenines possesses this band.

The significant differences in leg-musculature which have been discussed above (pp. 183-184) distinguish the carduelines from the New World finches and tanagers. Even the cardueline *Leucosticte* and the emberizine *Calcarius,* which resemble one another in general adaptations and in several myological features of the leg (p. 183), agree in significant features of the musculature with the respective groups to which they belong. The carduelines agree in the major features of leg-musculature with the ploceids which I studied.

The use of serological techniques in taxonomic work has two main advantages. The biochemical systems involved in such investigations seem to be relatively slow to change in response to external environmental influences, and the quantitative nature of the results obtained makes possible objective measurement of resemblances among species.

I have pointed out (p. 200) that the carduelines are excluded, serologically, from the distinct assemblage formed by the richmondenines, emberizines, and tanagers. Actually, the carduelines show less serological resemblance to this assemblage than do the estrildines, and most ornithologists agree that the Estrildinae are not at all closely related to the Richmondeninae, Emberizinae, and Thraupidae. *Molothrus,* representing a family (Icteridae) recognized as distinct from the Family Fringillidae, also more closely resembles the fringillid assemblage, serologically, than do the carduelines. Although the Carduelinae constitute a distinct group serologically, they show greater serological resemblance to the estrildines of the Family Ploceidae than to any of the other species tested. At least the carduelines and the estrildines form a group as compact as the subfamilies of the Fringillidae. Thus, the serological data correlate well with those obtained from the study of the leg-musculature.

Present systems of classification include the subfamilies Passerinae and Estrildinae in the Family Ploceidae. *Passer,* however, is less closely related to the estrildines serologically than are the carduelines, and is less closely related to the estrildines than *Molothrus,* an icterid, is to the fringillids. This raises a question as to the homogeneity of the Family Ploceidae as presently recognized by most ornithologists. If the Passerinae and the Estrildinae are placed in a single family, the serological divergence among members of this group is certainly greater than it is in the Family Fringillidae. Additionally, Beecher (1953:303-304) found that the estrildines possess a pattern of jaw-musculature different from those in other ploceids.

The combined evidence from jaw-musculature and serology has caused me to conclude that the estrildines should be excluded from the Family Ploceidae (see below).

In an attempt to clarify the relationships of the Fringillidae and allied groups, I here review briefly the evidence which has been presented. From his studies of jaw-musculature (1951a, 1951b, 1953) Beecher concludes that the Pyrrhuloxinae (=Richmondeninae), the Carduelinae, and the Thraupinae are closely related. He places these groups in the Family Thraupidae. He excludes the Emberizinae from this group and places them with the wood warblers in the Family Parulidae. He suggests that the estrildines constitute a family (Estrildidae) separate from the Family Ploceidae.

From his studies of certain features of the bony palate Tordoff (1954:25-26, 32) concludes that the richmondenines, the emberizines, and the tanagers have a common origin and places these groups in the Family Fringillidae. He excludes the carduelines from this assemblage, suggests that they are closely related to the estrildines, and includes them as the Subfamily Carduelinae in the Family Ploceidae.

In this paper I have presented data obtained from the study of certain features of morphology and biochemistry which I think are less subject to the influence of environmental factors than those features studied by recent workers. It is significant that the data obtained by use of serological techniques and those obtained from the study of leg-musculature point to the same conclusions. On the basis of these data I have drawn several conclusions concerning the relationships of the groups which I studied.

The richmondenines, emberizines, and tanagers are closely related and should be included in a single family, Fringillidae. The Carduelinae and the Estrildinae are closely related subfamilies. Although most recent classifications place the Estrildinae and Passerinae in the Family Ploceidae, the serological evidence indicates that these groups are not closely related. Beecher (1953:303-304) drew the same conclusion from his study of jaw-musculature (see above). I suggest, therefore, that the Carduelinae and the Estrildinae be placed in a family separate from the Ploceidae and that the name Carduelidae (rather than Estrildidae) be used for this group. At present, neither is an accepted family name. Because *Carduelis* Brisson 1760 is an older name than *Estrilda* Swainson 1827 and because *Carduelis* seems to be a centrally located genus in the family, I have chosen the former (although the International

Rules of Zoological Nomenclature do not specify that priority must apply in forming family names).

I have been unable to study any of the species included in the subfamilies Fringillinae (not Fringillinae of Tordoff, see 1954:23-24, and below) and Geospizinae of recent classifications; thus these groups have not been discussed above. Beecher (1953:307-308) includes *Fringilla* in the Subfamily Carduelinae; he includes the geospizines in a separate family, Geospizidae, and states that they are derived from the emberizines. Tordoff (1954:23-24) found that in features of the bony palate *Fringilla* and the geospizines resemble the emberizines and, on this basis, includes them in the Subfamily Fringillinae.

The Dickcissel, *Spiza americana*, possesses certain features which merit special discussion. Beecher (1951a:431; 1953:309), on the basis of jaw-musculature, considers it an icterid. To be sure *Spiza* is in many ways an aberrant member of the group to which it is now assigned (Subfamily Richmondeninae). *Spiza*, serologically, is closely related to all species of the richmondenine-emberizine-thraupid assemblage. Within this assemblage its nearest relatives are the richmondenines. *Spiza* differs from the other richmondenines studied and resembles the emberizines and tanagers in the possession of the muscular band which extends from the *pars interna* of the *m. gastrocnemius* around the front of the knee. This band, in *Spiza*, is smaller, however, than in any of the other species. No icterid dissected possesses such a structure. Tordoff (1954:29) states that *Spiza* is typically richmondenine in palatal structure and makes the suggestion, with which I agree, that *Spiza* is a richmondenine and may be closely related to the ancestral stock which gave rise to the fringillid assemblage. The serological position of *Spiza*, approximately equidistant from the other fringillids (Figs. 22, 23), and the presence of the small muscular band around the front of the knee constitute evidence supporting the central position of *Spiza*.

After consideration of evidence from the studies of external morphology, ethology, myology, osteology, and serology, I propose here an arrangement of the groups which I have studied and submit for comparison the arrangements (of these groups) proposed by Beecher and Tordoff. The names of subfamilies that I have been unable to study are included in my classification and are placed in brackets.

Here proposed:	Proposed by Tordoff (1954) on the basis of the bony palate:	Proposed by Beecher (1953) on the basis of jaw-musculature:
FAMILY PLOCEIDAE	FAMILY PLOCEIDAE	FAMILY PLOCEIDAE
[Subf. Bubalornithinae]	Subf. Bubalornithinae	
Subfamily Passerinae: distinguished from the Estrildinae by patterns of jaw-musculature (Beecher, 1953:303-304) and on the basis of comparative serology of saline-soluble proteins.	Subfamily Passerinae	Subfamily Passerinae
[Subfamily Ploceinae]	Subfamily Ploceinae	Subfamily Ploceinae
[Subfamily Viduinae]	Subfamily Viduinae	Subfamily Viduinae
FAMILY CARDUELIDAE		
Subfamily Estrildinae: similar to the Carduelinae in features of the bony palate and habits (Tordoff, 1954:18-22) and in patterns of leg-musculature and comparative serology of saline-soluble proteins.	Subfamily Estrildinae	FAMILY ESTRILDIDAE
Subfamily Carduelinae: distinguished from the Fringillidae by features of the palate, geographic distribution, migration patterns, and habits (Tordoff, 1954: 14-18) and by patterns of leg-musculature and comparative serology of saline-soluble proteins.	Subfamily Carduelinae	[In Thraupidae below]
FAMILY FRINGILLIDAE: all members of this family show similarities in features of the bony palate (Tordoff, 1954: 22-23), patterns of leg-musculature, and in comparative serology of saline-soluble proteins.	FAMILY FRINGILLIDAE	FAMILY PARULIDAE Subfamily Parulinae Subfamily Emberizinae
		FAMILY THRAUPIDAE
Subf. Richmondeninae	Subf. Richmondeninae	Subfamily Pyrrhuloxiinae
Subfamily Thraupinae	Subfamily Thraupinae	Subfamily Thraupinae
Subfamily Emberizinae	Subfamily Fringillinae (including Emberizinae and Geospizinae)	[In Parulidae above]
[Subfamily Fringillinae]		Subfamily Carduelinae
[Subfamily Geospizinae]		

SUMMARY

It has long been recognized that the Family Fringillidae includes some dissimilar groups. Specifically, the relationships of the subfamilies Richmondeninae, Emberizinae, and Carduelinae of the Family Fringillidae are poorly understood. Data from two recent studies, one on patterns of jaw-musculature and the other on features of the bony palate, emphasize the dissimilarity of these subfamilies but have given rise to conflicting concepts of the relationships of subfamilies within the Family.

This paper reports the results of studies involving morphological and biochemical features that I consider less sensitive to external environmental factors than are features which have been studied previously. Patterns of leg-musculature were chosen for study because earlier work showed that muscle patterns in the legs of passerine birds are highly stable and vary but little. Variations, therefore, which are consistent in separating groups of species should be significant. Serological techniques were used because the biochemical systems involved seem to be relatively slow to change in response to environmental influences and because the data obtained may be used in a highly objective manner to measure resemblance among species.

Individual differences in the patterns of leg-musculature were found to be slight and involved mainly the sizes and shapes of muscles. For this reason variations involving origin, insertion, or relative position of a muscle, were judged significant. In leg-musculature the Richmondeninae, the Emberizinae, and the Thraupidae resemble one another closely. Several differences in muscle pattern were found, however, which distinguish these groups from the Carduelinae. The leg-musculature of the carduelines closely resembles that of the Ploceidae.

Serological techniques involved the extraction of saline-soluble proteins from the tissues of the species to be studied. These extracts were carefully processed and were used as antigens. Formolization of the antigens was necessary as a means of preventing denaturation of the proteins by enzymatic activity. Antisera were produced in rabbits. The method of testing involved turbidimetric analysis of the precipitin reaction. Utilizing the values for the precipitin tests a model was constructed which showed the relationships of the eleven species used in these tests. From a study of the model and the data used in its construction, it was determined that the Richmondeninae, Emberizinae, and Thraupidae constitute an assem-

blage distinct from the other species studied. The Carduelinae are excluded from the assemblage and serologically are most closely related to the Estrildinae. The estrildines, serologically, do not closely resemble *Passer,* Subfamily Passerinae, although recent classifications place these two subfamilies in the Family Ploceidae.

Upon consideration of all evidence now available—from external morphology, ethology, myology, osteology, and serology—several hypotheses regarding the relationships of the groups studied are set forth. The richmondenines, emberizines, and tanagers are closely related subfamilies and are here included in the Family Fringillidae. The Estrildinae and Carduelinae are closely related subfamilies, but neither group is closely related to the Passerinae. The estrildines and carduelines, therefore, are placed in a separate family, the Carduelidae. In some ways, *Spiza* is an aberrant member of the Subfamily Richmondeninae but should be retained in that subfamily. It is suggested that *Spiza* is a primitive richmondenine closely related to the ancestral fringillid stock.

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25-4632

(Continued from inside of front cover)

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Index. Pp. 605-638.

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Index. Pp. 651-681.

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18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.

(Continued on back of cover)

(Continued from inside of back cover)

24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-317. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.
2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
6. Distribution of Some Nebraskan Mammals. By J. Knox Jones. Pp. 479-487. April 21, 1954.
7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
8. A new subspecies of bat (Myotis velifer) from Southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.
9. Mammals of the San Gabriel Mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.

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2. Myology and Serology of the Avian Family Fringillidae, a Taxonomic Study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

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BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
1956

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(Continued on inside of back cover)

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Henry S. Fitch

CONTENTS

	PAGE
Introduction	215
Methods	217
Habitat	218
Seasonal activity	223
Temperature	224
Reproduction	229
Growth	237
Regeneration and recovery from injury	244
Molt	246
Numbers	247
Territoriality	250
Food habits	259
Predation	263
Parasites	267
Summary	267
Literature cited	271

INTRODUCTION

Intensive observations were made over a period of six years on a colony of collared lizards living on an area of less than an acre on the University of Kansas Natural History Reservation in the northeastern corner of Douglas County, Kansas. Supplementary data were obtained from populations in other parts of eastern Kansas. Also, I have collected and observed this species in Oregon, California, Nevada, Utah, Arizona, New Mexico and Texas.

Although no field study of the collared lizard has been made previously, literature dealing with this species has provided background information, and I have summarized the more pertinent statements bearing on various phases of the life history. These statements are based upon the observations of various workers, at localities well scattered throughout the species' geographic range. I am fully cognizant that the species is geographically variable, both morphologically and probably also in its behavioral responses and physiological adaptations to local environments. Changes in all these characters that occur in different parts of the range, probably do not correspond well either with political boundaries, nor, for that matter, with the range limits of the recognized subspecies.

The collared lizard is one of the larger kinds of lizards occurring in the United States. Because of its large size, bright colors, and extensive geographic range, it is better known to the public than most kinds of native reptiles. It is often used for dissection in courses in comparative anatomy, serving as an example of a typical reptile. Otherwise the economic importance seems to be slight. The collared lizard's hardiness in captivity, and its life cycle, much shorter than those of most other reptiles, suggest its possible usefulness as a laboratory animal. With proper technique it might be artificially propagated, and used for studies in genetics, physiology, bacteriology and other fields.

The collared lizard is a medium-sized representative of the saurian family, Iguanidae, which is especially well represented in the arid southwestern part of North America. The head is especially large and wide, with unusually powerful jaws. The scalation is fine and granular. There is a prominent gular fold. The hind legs are large and strong. Bipedality, known in various desert-living lizards, is especially well developed in the collared lizard. The tail, which is almost twice the length of the combined head and body, is an aid to balance in running and leaping and lacks the fragility which characterizes the tails of most lizards, including those of closely related iguanid genera.

The collared lizard has three recognized subspecies: *C. c. collaris* occurring from southern Missouri and northern Arkansas west through Kansas, Oklahoma, Texas, and western New Mexico; *C. c. baileyi* in New Mexico, Arizona and parts of eastern California, Nevada, western Utah, southern Idaho and southeastern Oregon; and *C. c. auriceps* in the Upper Colorado and Green River basins of eastern Utah and adjacent Colorado. *C. dickersonae* and *C. insularis* are closely related insular forms in the Gulf of California, while *C. reticulatus* of extreme southern Texas and adjacent Mexico is separable by trenchant characters of pattern, lepidosis and ecology.

The closely related leopard lizard has been generically separated from the collared lizards by Smith (1946: 158) as *Gambelia wislizenii,* but this proposal has not been universally accepted. In advocating it, Smith indicated numerous morphological differences between *Crotaphytus* and the monotypic *Gambelia.* An additional difference that should be considered in any final judgment as to the generic distinctness of the two groups is the trend in sexual dimorphism. In *Crotaphytus* as in most iguanids the male is notably larger than the female, and more brightly colored, with distinctive pattern. In *Gambelia* there is even greater size disparity between the sexes, but the female is the larger, and there is little or no difference in color or pattern.

The ten collared lizards that were the nucleus of the colony studied were collected by a graduate student on the bluffs north of the Kaw River, approximately ten miles east of Manhattan in Pottawatomie County, Kansas, on April 29, 1949, and a few days later were released at the site of an old limestone quarry on the University of Kansas Natural History Reservation. This 590-acre tract had been set aside as a natural area in July 1948, with an established policy of keeping to the minimum disturbance from human activities, and protecting the plant and animal life already present. So far as known the "introduction" of these collared lizards is the only deviation, animalwise, from that policy. Fortunately the establishment of the colony of collared lizards has had negligible effect on the over-all ecology. The number of individuals has remained small (never more than six adults) over several generations and the colony has been closely limited to the vicinity of the quarry. In this region the collared lizard is an indicator species characteristic of an early stage in xeroseral succession. The small colony at a site convenient for study, on the margin of the species' range has provided unusually favorable opportunity for attaining understanding of this lizard's ecology.

Two other deviations from the policy established in 1948 are recorded here not because of any bearing on collared lizards but because of possible bearing on results obtained from future studies: (1) a heavily eroded and nearly barren field (see Fig. 10) that had been cultivated previous to 1948 was seeded to native grass in April, 1949; (2) a pond that caught run-off from this field was deepened in the winter of 1953-54 by removing silt. It is expected that the pond will not soon again silt up now that unnatural erosion has been stopped.

METHODS

Collared lizards were studied by regular observations on free individuals under natural conditions. The area occupied could be checked in a few minutes, and most or all of the lizards could be recorded if they were active. Or if none was in evidence, it could be safely assumed that unfavorable weather conditions were causing them to remain in sheltered places.

Direct observations provided information concerning the movements, territoriality and other social behavior, hunting, feeding and escape reactions. The few adults present at any one time could usually be individually recognized at a distance. Each lizard, nevertheless, was marked by clipping one or two toes, and these marks visible at distances up to ten feet or more, served to verify the identity of the individual. Sight records were often obtained without recapturing the lizard. More often it was recaptured, and the snout-vent length, tail length, weight, exact location, stage of molt, coloration, ectoparasites, and body temperature were routinely recorded. By July, 1954, one marked collared lizard had been recorded a total of 101 times in six different years; its records constituted the most complete individual life history yet obtained on the Reservation, among the thousands of individuals of dozens of different species studied.

The measurements of live lizards in this report are not comparable to the same measurements made on preserved specimens because of the shrinkage amounting to a loss of several per cent in dimensions in the latter. The amount of loss is variable, depending on the type of preservative, and the position in which the specimen hardens. The live specimens could be measured more accurately than preserved specimens; the margin of error was occasionally as much as three per cent, but averaged less than one per cent.

Several dozen traps for reptiles, both pitfalls and wire funnel traps (Fitch, 1951: 78), were used in the area occupied by the colony, and on rare occasions these lizards were caught in them. Occasionally, also, one was captured by hand, with a quick grab after a slow and stealthy approach. This method was seldom successful when a lizard was fully warmed and active, because its reflexes were then quicker by far than those of a person. A more effective method was to noose the lizard with a fine copper wire attached to the end of a straight five-foot stick. My improved dexterity in the use of such snares was partly offset by the lizards' experience in learning to avoid them. Hatchlings were most difficult to noose, however, and for them wire of exceedingly fine gauge was used, while for larger individuals heavier wire was more effective.

HABITAT

Many zoologists who have collected collared lizards or have observed them in the field, have published brief but significant statements concerning the habitat conditions under which the species occurs locally. Statements from the literature, assembled below, in general, bear out my own observations concerning the types of habitat occupied in different regions, climates and plant associations within the geographic range.

The evidence indicates that ordinarily, but not invariably, collared lizards are limited to rocky situations, though not to any one type of rock, as regards geologic origin, composition or color; that rocks and boulders within a wide size range, from a few inches to several feet in diameter, meet the requirements; that in the western part of the range the species tends to inhabit more rugged and broken terrain than it does in the east where it may live in prairies or even in open woodland.

Ruthven and Gaige (1915: 17) in northeastern Nevada found collared lizards only at the rocky summit of the Cortez Range, and in northwestern Nevada, Richardson (1915: 406) found them restricted to rocky hillsides among deposits of volcanic rock and tuff at 4500 feet. In the Toyabe Mountains of central Nevada, Linsdale (1938: 25) found them on the lower slopes (6500 to 7500 feet), where the ground was conspicuously strewn with medium- or large-sized rocks. The same author (1940: 214) quoted my own field notes describing the habitat in Nevada: In small rocky ravines along the sides of ridges at Pahranagat Valley, Lincoln County; and at Cliff Spring in Nye County, in boulder-strewn gravelly areas of the foothills, and occurring out into the sagebrush flats along rocky ravines. Near Currant, Nye County, Bentley (1919: 88) found these lizards on the large flat rocks of a steep hillside.

Taylor (1912: 346), in northern Humboldt County, Nevada, recorded ten on the top of a steep sided rocky ridge, and one at the base of the ridge. In adjacent Malheur County of southeastern Oregon, Brooking (1934: 94) found the collared lizard common in rocky places where there was sand and sagebrush.

In southern California, Atsatt (1913: 33) found it in both rocky and sandy spots in the San Jacinto Mountains. Cowles (1920: 64) found it on rocky hillsides. Klauber (1939: 85) stated that it preferred areas with scattered rocks to those which were essentially masses of rock. Camp (1916: 521) found that in the Turtle Mountains these lizards inhabited the rocky slopes, and lived also among rocks about the bases of the range, but not in the open desert. Johnson, Bryant and Miller (1948: 258) noted that in the Providence Mountains region these lizards were in unshaded rocky places between 4500 and 5700 feet, and that they sprawled on tops of large boulders, never far from the rock crevices that served as shelter. Shaw (1950: 31) stated that in San Diego County, it is normally an inhabitant of boulder-strewn slopes of desert hills and mountains.

Stejneger (1893: 165) stated that the western collared lizard lived among rocks, frequently in canyons, and is most common in the desert ranges. Van Denburgh (1922: 113-114) stated that those he had observed were always on tops of boulders, and he quoted Slevin's observation that in southeastern Arizona this was a rock-loving species, appearing on the tops of boulders late in the afternoon. In southern Arizona, Ruthven (1907: 13) found it in the Atriplex association of the plains and in the sotol-ocotillo association of the foothills. In the Roosevelt Reservoir area of central Arizona, Little (1940: 262) found it in the zones of semi-desert and chaparral-woodland.

In New Mexico, Little and Elbert (1937: 219) recorded five on the Jornada Range, four of which were on rocky foothills and one on the plain. Lewis (1951: 182) found it in the Tularosa Basin area mainly at the edges of the foothills in rocky places. In western Colorado along the southern boundary, Maslin (1947: 7) found it in canyons and other rocky areas.

In Texas, Cope (1900: 251) stated that it is common among rocks and in open woods. On the Stockton Plateau, Milstead, Mecham and McClintock (1950: 552) recorded six in the cedar-ocotillo association (described as occupying the mesa slopes, and having extensive rock coverage but only sparse vegetation), and one from the mesquite-creosote association of the valley. Smith and Buechner (1947: 7) listed it as one of the several species of lizards occurring on the Edwards Plateau of west-central Texas, but limited on the east by the Balcones Escarpment which marks the eastern edge of this plateau.

In Kansas, Burt (1927: 3) found it to be the most common lizard in Riley County, where it occurred about rock ledges and stone quarries. Smith (1950: 169) stated that in the prairies the species was restricted to rocky areas or canyons and reached maximum abundance on the limestone-capped hills of the central part of the state. Householder (1916: 11) wrote that it was most abundant along hilltop limestone ledges in the Flint Hills, and was rarely found in the immediate vicinity of woods. In Jackson County, western Missouri, Anderson (1942: 207) recorded it to be common around limestone ledges.

On June 17, 1951, four miles southwest of Garnett, Anderson County, Kansas, I saw two dozen collared lizards in about two hours' collecting. This was in a rolling prairie habitat, strewn with numerous flat rocks of varying sizes up to two feet or more in diameter. There were scattered clumps of fragrant sumac (*Rhus trilobata*) with but little other woody vegetation. False indigo (*Baptisia*), prickly pear (*Opuntia*) in low patches, and spiderwort (*Tradescantia*) were among the more conspicuous herbaceous plants. I found these lizards at several other places within a few miles of Garnett. Some were in rocky places in low, sparse second-growth oak-hickory woods. One colony in an especially dense population, was at a large quarry.

In Kansas the range of the species is mainly across the southern part, and north in the central part nearly to the northern edge. Known localities of natural occurrence nearest to the Reservation are approximately 40 miles east (in Missouri), 60 miles west, and approximately 60 miles south in drier and more open rock habitat. As these lizards are large and conspicuous and as the northeastern part of Kansas has been thoroughly searched by collectors, it seems doubtful whether the species extends farther north or east. The most obvious limiting factor is the increasing rainfall farther east, with more rank growth of vegetation limiting the extent of the habitat even in favorably rocky situations. In earlier times the species must have been more generally distributed in eastern Kansas and perhaps in western Missouri, to have reached these marginal localities. There is ample evidence that under original conditions, before eastern Kansas was settled, woodlands were less extensive there, being held in check by prairie fires, and perhaps by browsing of native mammals, so that there must have been exposed rock outcrops on south slopes similar to those in situations where the species still occurs, farther south and west. Perhaps the species was much more generally distributed in this region before the time it was settled about 100 years ago. Later, the control of prairie fires permitted trees and shrubs to invade dry hillsides and shade the rocky situations so that these no longer provided favorable habitat. In Douglas County and the adjoining counties of northeastern Kansas, even in situations that appear to be favorable, the species has not been found. It may have reached its present northeastern limit in a time of warmer and drier climate, and may have undergone retrenchment long before this part of the country was altered by settlement. The known locality records suggest that the distribution in Kansas is discontinuous. An extensive area of the Arkansas River valley in the Great Bend region is devoid of records. Even in the general areas that are most favorable for these lizards, stations of occurrence may be more or less widely separated by intervening areas where the habitat does not exist.

The localities of occurrence in Jackson County, Missouri, mentioned by Anderson (1942: 207) seem to represent the northeastern corner of the geographic range, and evidently are occupied by small relict populations well separated from others.

The colony studied at the Reservation was closely confined to the area of an old limestone quarry, on a southward projecting spur of a hilltop (Pl. 4, fig. 3). The Oread limestone is exposed as an outcrop several feet thick along hilltop edges throughout this general area. The rock had been removed from an area approximately 400 feet long and 50 feet wide, exposing a nearly flat rock surface, with sparse low vegetation of ragweed and lespedeza. Along the upper edge was a nearly vertical south- and southeast-facing rock surface 3 to 10 feet high, with numerous cracks and fissures. From the base of the outcrop to the nearby flat there was a steep slope of accumulated rock-debris and soil averaging approximately 15 feet wide and supporting a variety of herbaceous vegetation, especially sweet clover (*Melilotus*), stickleaf (*Mentzelia*) and saplings of elm and cottonwood.

The collared lizards stayed mostly along the top of the outcrop at certain favorite spots, and moved between them by the most direct routes. On the hilltop above the outcrop thick brome grass and other herbaceous vegetation with scattered shrubs grew nearly to the edge. The exposed top of the outcrop and the shallow, bare soil adjacent to it provided lookouts and travelways that were essential features of the lizards' habitat. Deep crevices in the outcrop provided the retreats into which the lizards escaped in time of danger or retired for periods of inactivity. The lizards run swiftly over barren soil and rock but cannot move rapidly through thick grass. Ordinarily they avoided it, except for short dashes into it to obtain insect prey. The sloping rocky ground below the outcrop was also used regularly by them. Certain large boulders were favorite basking places, and the shrubs and weeds provided shade on hot days. The open flat was much less used by the lizards. In their foraging they sometimes made short dashes onto it from their lookouts along the main outcrop. Late in the summer, when ragweed on the flat had matured, and grasshoppers were abundant there, the lizards often left their usual basking places along the outcrop to forage on the flats.

Because the collared lizard prefers open, rocky situations, and spends much time basking in the open, it might be expected to show some tendency to match the color of its surroundings. Several observers have commented on this tendency to develop a protective coloration. The discontinuous nature of the rocky habitat, with many small populations wholly or partly isolated from others, seems to have promoted the differentiation of many local color variants. Stejneger (1893: 165) mentioned the dark color of these lizards on the black lava in Diamond Valley between St. George and the Upper Santa Clara Crossing in southwestern Utah.

Franklin (1913: 2) noted that on the Painted Desert in northern Arizona, areas of black lava-rock were inhabited by collared lizards of darker hue than those inhabiting nearby paler rock formations.

In New Mexico, Lewis (1951a: 182; 1951b: 311) noted the prevailingly black hues of specimens from different areas of the black Malpais lava, both in the Tularosa Basin and along the Mexican border. In the same general region Ruthven (1907: 513) noted colors harmonizing perfectly with the light soil. In other parts of New Mexico also, I have observed populations of unusually dark individuals on areas of black volcanic rock.

In the subspecies *auriceps* of eastern Utah, the coloration does not seem to aid in concealment; both the bright green of the body and the yellow of the head contrast with the prevailingly red rocks upon which the lizards perch.

In general, limiting factors for this species of lizard are:

1. Presence of boulders within a wide range of size, from a few inches to a few feet in diameter, providing lookouts and basking places that permit varying orientation for thermoregulation, and also providing escape shelter from natural enemies.
2. Vegetation sparse enough so that sunlight is readily available, so that a view of surroundings from rock perches is not obscured, and so that running is not impeded.
3. A food supply of large, terrestrial, and diurnal insects.
4. A climate with high summer temperature and little cloudiness, permitting maintenance of high body temperature by insolation.

SEASONAL ACTIVITY

Compared with other kinds of reptiles that live in Kansas, the collared lizard has high temperature thresholds for various types of activity. At temperatures up to 10° C. it is incapable of locomotion and completely helpless. As a result it has a shorter growing season than many other reptiles living in the same areas. For the colony on the Reservation earliest recorded activity was as follows: April 26, 1950 (all or most of the individuals present were active); May 12, 1951; May 5, 1952 (some did not emerge till May 7, and others not until May 10); April 2, 1953 (a single individual prematurely emerged—no more activity subsequently until April 26); April 6, 1954 (several not until the following day) and April 21, 1955. The emerging population in spring consists of: (1) adults, including all those that are more than a year old and have hibernated two or more times; (2) young that hatched late the preceding summer and were active for only a few weeks before retiring into hibernation. These young vary widely in size. This is especially true when measurements of young in different years are compared. The stage of development attained by the time the first hibernation begins is determined largely by the weather.

Several weeks after emergence from hibernation the breeding season begins and in late May and June most adults are in pairs. Of young hatched in the preceding summer some mature sexually in time to participate in the annual breeding season but some fail to mature in their first year. Within a few days after insemination, the pregnant females develop scarlet spots on each side of the body, and these persist for several weeks after the eggs are laid, usually in June or early July. After egg-laying, adults of both sexes are less in evidence than in spring and early summer because of a tendency to desert conspicuous territorial perches used in spring in favor of more sheltered and shaded spots and partly because of a tapering off of activity, as the lizards remain underground and inactive. Whether there is true aestivation is unknown, but old adults are rarely seen after early August. In late July and early August the individuals most in evidence are the young of the previous summer, which normally are approaching average adult size at the age of approximately a year. Hatchlings appear usually in August or September (in 1951 none appeared until late October). By the time the hatchlings have emerged both the adults and the year-old young have become relatively inactive and are rarely seen. The early growth of hatchlings is exceedingly rapid, and by the time they retire into hibernation at an age of a few weeks they may be approximately half-grown (in bulk). Their activity normally continues until some time in late September or October when it is terminated by low night-temperatures. Latest recorded occurrences of adults and hatchlings in five different years are contrasted in Table 1.

TABLE 1.—LATEST RECORDED DATES OF ACTIVITY FOR YOUNG AND ADULTS IN SIX DIFFERENT YEARS.

	1949	1950	1951	1952	1953	1954
Adult...	Aug. 25	Sept. 8	Sept. 6	Aug. 30	Sept. 1	Aug. 27
Young..	Sept. 29	no records	Oct. 20	Oct. 2	Oct. 10	Sept. 28

TEMPERATURE

Limit of tolerance to low temperature is unknown but probably is near freezing. Much of the geographic range of the collared lizard has moderate to severe winter climates, with air temperatures frequently below 0° F. These lizards are not efficient burrowers and since they live in rocky places they probably depend to a large extent on natural crevices.

In the winter of 1953-4, a thermometer was installed at a depth of 30 inches in a crevice of the rock ledge on the wooded slope adjacent to the quarry but at approximately 20 feet lower elevation. The minimum temperature reached at this site was approximately 3° C. It is doubtful whether any crevices as deep as this were available where the collared lizards hibernated; they probably withstood slightly lower temperatures.

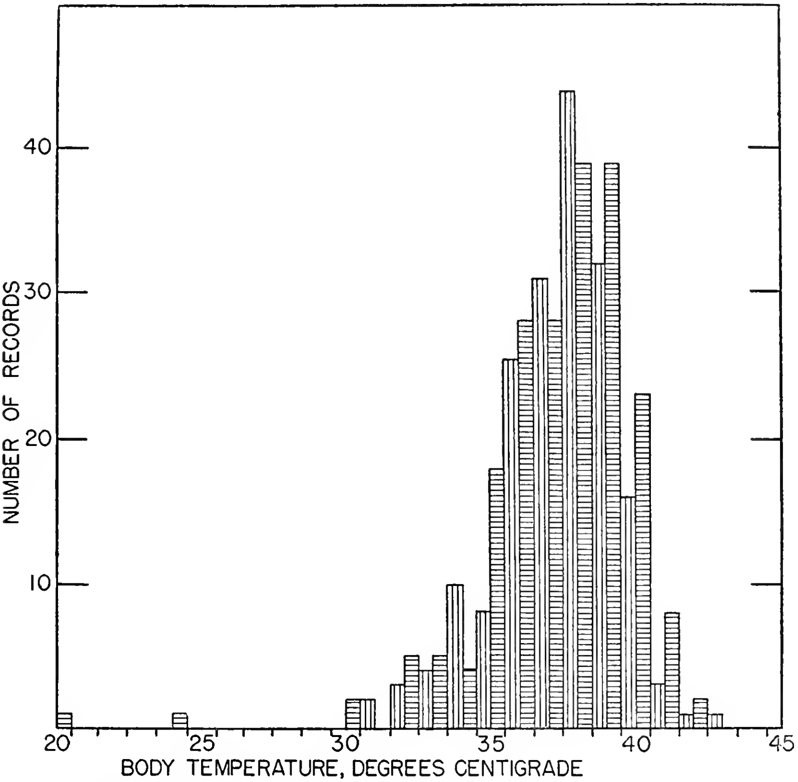


FIG. 1. Histogram showing body temperatures in active collared lizards under natural conditions. Males (columns with vertical bars) and females (columns with horizontal bars) are shown separately. For both, optimum level seems to be between 38° and 39° C, and most of the records are concentrated near this level.

On April 20, the body temperature of an adult male was 6° C. When handled, he roused from his torpor sufficiently to open his eyes, squirm slowly, and hiss with each expiration. When placed on a table, and stimulated by poking he could rise and stand erect on all four legs for a few seconds, but he was incapable of locomotion, and would soon sink down in torpid sleep. While being handled, he opened his mouth in threat. A finger placed in his open mouth elicited biting response after a delay of several seconds. The lizard exerted pressure only briefly, but resumed it immediately

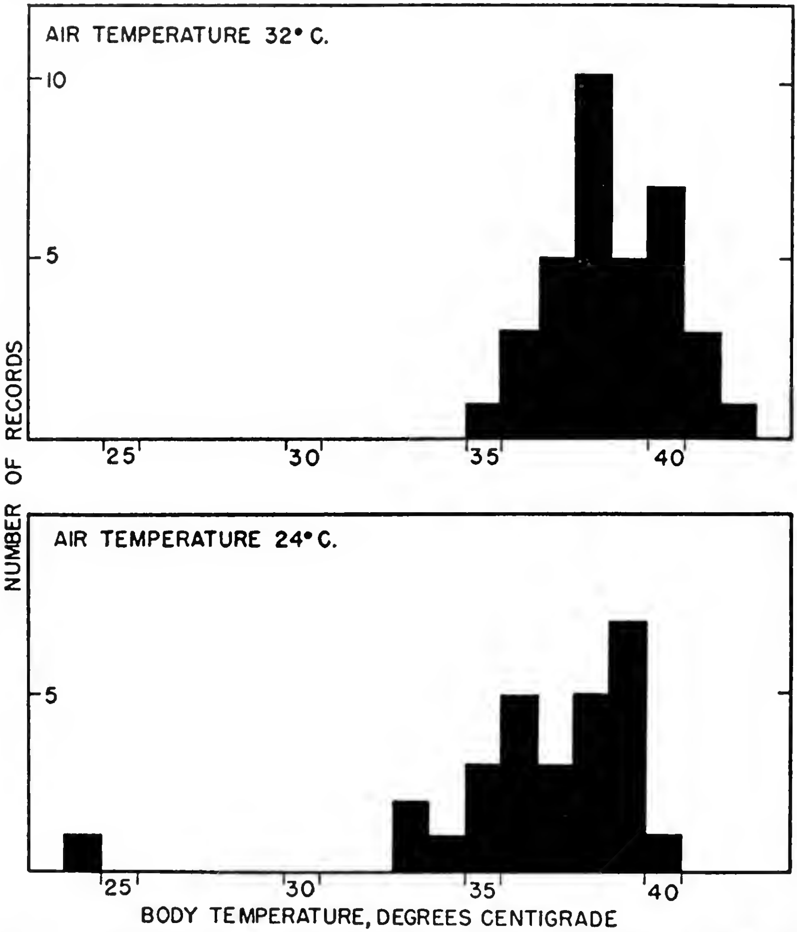


FIG. 2. Histogram comparing body temperatures in collared lizards caught at air temperatures of 24° C and 32° C. Both groups tend to maintain body temperatures approximating the optimum level, but averages and extremes are slightly lower at the lower air temperature.

when attempt was made to withdraw the finger, which was extricated with difficulty. The lizard's coloration was dull, dusky grayish brown with no green showing.

On April 9, 1953, one that had been kept for two days in an unheated room was examined at 11.8° C. He was semi-torpid, and when stimulated was barely capable of locomotion, taking only one or two steps with the body dragging on the ground, and then lapsing again into lethargy and shutting his eyes. Responses were similar to those of a five-lined skink (*Eumeces fasciatus*) at only 1.5° C., emphasizing the dependence of the collared lizard on higher temperatures. When handled, the collared lizard attempted to bite and kept his body inflated with air. Color was dull, predominately dark brown, with faint greenish tint on lower parts of sides and on legs. The dorsal white spots on the body were mostly dull and inconspicuous, suffused with brown.

As collared lizards are most characteristic of desert regions their preferred temperature is high. In those that were caught at the quarry, body temperature, taken rectally, at the moment of capture, ranged from a low of 20.7° C. to a high of 43.3° C. Ordinarily during activity, body temperature is maintained within a much narrower range (see Fig. 1). Cowles and Bogert (1944: 280) obtained body temperatures of several short-nosed leopard lizards (*Gambelia wislizenii silus*) that were active under natural conditions, and the average was 38.7° C. Evidently the leopard lizard is similar to the collared lizard in its temperature preference. Of 513 recorded body temperatures of the collared lizards, 87.1 per cent were within the six-degree range, 35° to 41°, and more than half, 55.8 per cent, were within the three-degree range from 37° to 40°, and these included individuals caught over a wide range of air and substrate temperatures. It seems that the optimum for collared lizards lies within this relatively narrow margin. By thermoregulatory behavior each individual tends to keep its body temperature near the optimum even though this may impose severe limitations on its activities. Figure 2 compares the lizards' body temperatures at two different air temperatures, one near the lower limit of their usual activity range (24°) and the other near the upper limit (32°). Preferred temperatures may differ slightly in the sexes, but this is not conclusively shown. The earliest emerging individuals in spring are males. A disproportionately large number of the body temperatures above 40° C. were those of females (Fig. 1).

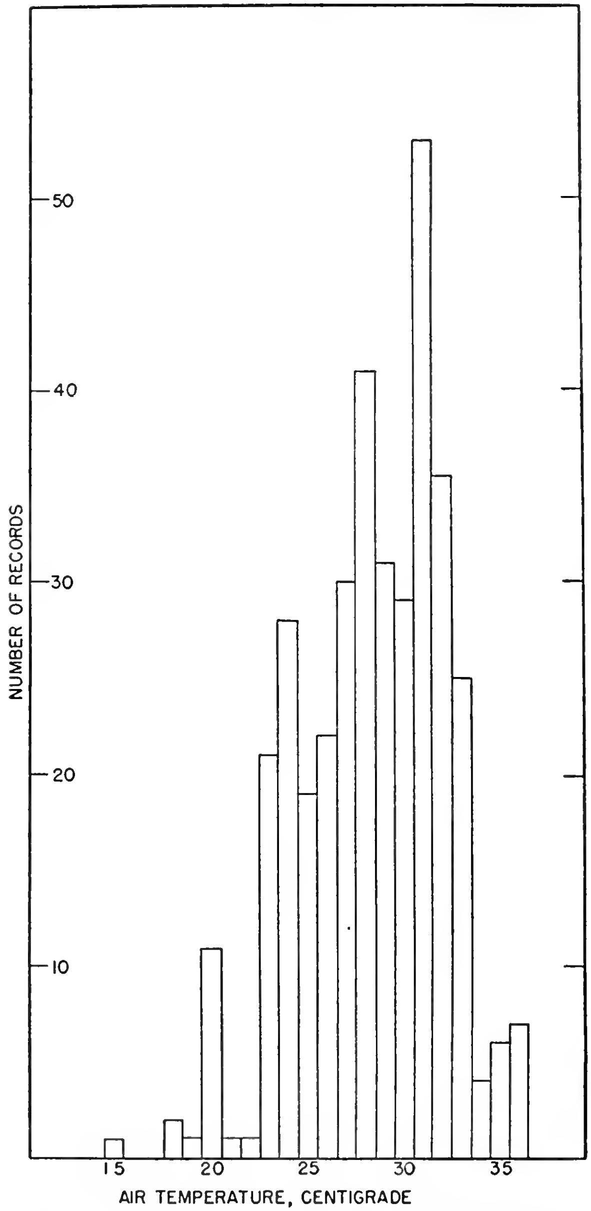


FIG. 3. Numbers of captures recorded at different air temperatures, grouped in one degree intervals. Optimum air temperature for activity is between 23° and 34° C, several degrees below the preferred body temperature, which is normally maintained by insolation.

PLATE 3

FIG. 1. Adult male collared lizard, in bright sunshine on a warm day, standing high to avoid contact with the heated rock surface; ⅓ natural size.

FIG. 2. The same adult male shown in Fig. 1, seeking shelter in shade of a jutting rock to avoid overheating; ⅓ natural size.

FIG. 3. Adult male collared lizard eating a grasshopper; the prey is secured with a sudden rush, killed with a hard bite, and swallowed with a few rapid gulps; a little less than ⅓ natural size.

PLATE 4

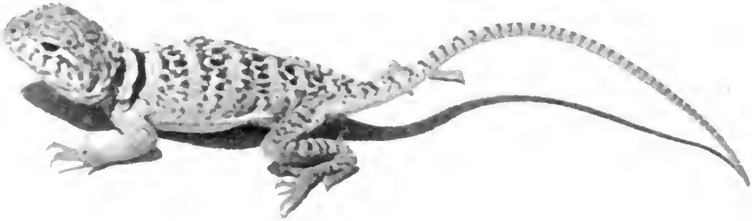


FIG. 1. Hatchling showing color pattern different from that of adult; there are prominent light cross bars on the body, and dark, rounded dorsal spots; slightly larger than natural size, August 6, 1953.

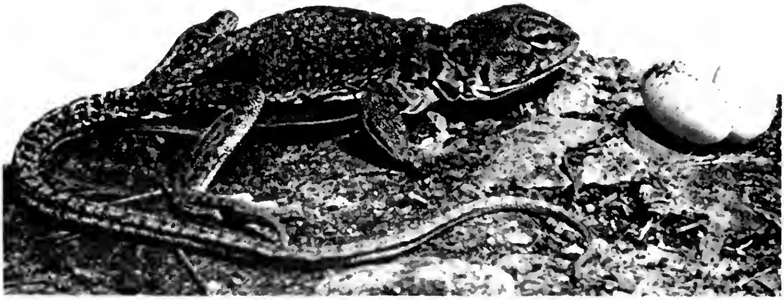


FIG. 2. Adult female from Coconino County, Arizona, with two freshly laid eggs of a clutch of four; ⅗ natural size, July 20, 1950.

FIG. 3. Limestone outcrop at a deserted quarry, the habitat of the colony of collared lizards studied. The lizards stayed on or near the outcrop and the litter at its base. They rarely ventured onto the flat in the foreground, and never wandered more than a few yards into the high grass and weedy vegetation of the hilltop. The rock outcrop shown extends for many miles along hilltop edges in this section of land and the sections adjacent to it. Except at the quarry, however, the outcrop is shaded by trees and brush rendering it uninhabitable to the collared lizards.

PLATE 5

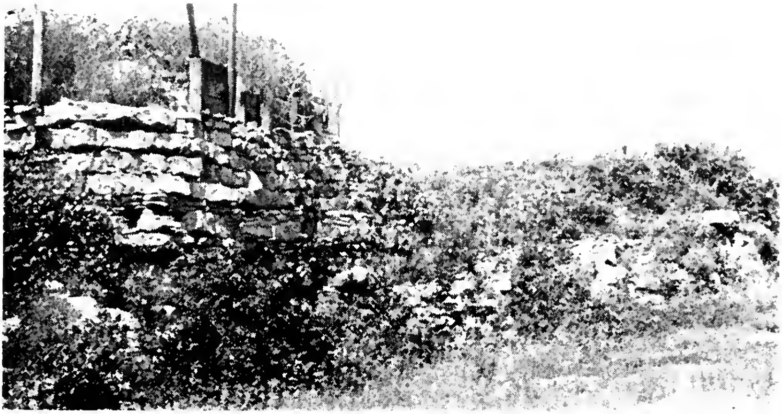


FIG. 1. Rock wall near middle of old quarry inhabited by a colony of collared lizards. Overhanging boulders at the top of the outcrop, on the extreme right and the extreme left were favorite territorial look-outs. June 16, 1953.

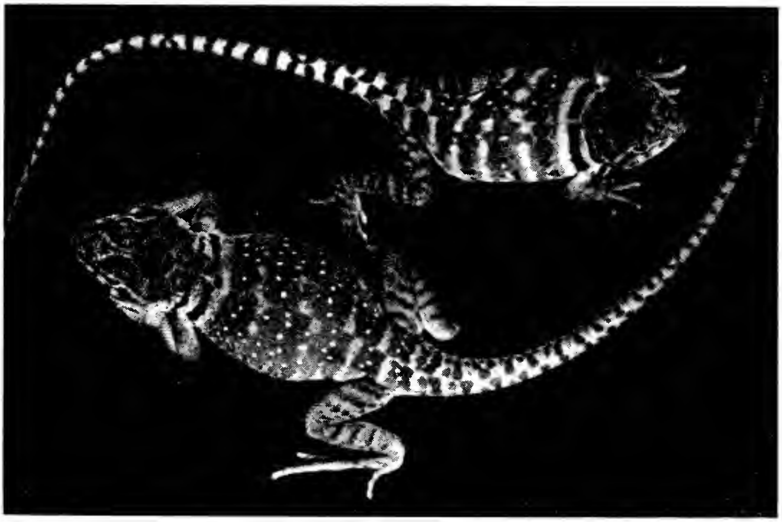


FIG. 2. Juvenal collared lizards beginning to show sexual differences in color and pattern. The female (above) is approximately two weeks old and still retains the hatchling pattern but markings are less sharply defined than they were at first. In the male (below) at an age of approximately three weeks, the pattern is in a stage transitional between that of the hatchling and that of the adult. White dots have become prominent in the dorsal pattern, the pale transverse bands have almost disappeared, and the dark dorsal spots have fused and lost their original outline. Approximately natural size, September 1, 1953.

PLATE 6

FIG. 1. Four year old adult female; the pattern has become dull, with the original markings obscured. This individual was recorded a total of 101 times in six different years; ½ natural size, August 15, 1953.

FIG. 2. Courting male (left), moving around the female with slow, loose-jointed slithering gait, with body dorsoventrally flattened and gular pouch distended; ½ natural size.

Collared lizards were found active over a wide range of air temperatures (Fig. 3), from a minimum of 13.5° C. to a maximum of 36° C.; however, 91 per cent of the records were at air temperatures in the eleven-degree range between 23° and 34°, and it is evident that most activity is limited to this temperature range. More than half the records were at air temperatures within the range 28° to 33°. By the time air temperature has risen to the lizards' optimum body temperature or near it (37° or 38°), the lizards seek shelter undeground as they prefer much lower air temperatures and depend on insolation for warmth. Soil receiving direct sunlight attains a surface temperature far higher than the temperature of the air. For instance, on July 11, 1954, when the air temperature was 40.5° C., I recorded 60° C. in the soil at a depth of a quarter inch. Actual surface temperature was probably well above this figure, but it could not be measured with available instruments. Under such conditions the environment above ground is hostile, and the lizards, if they are active at all are closely confined to shaded spots. On cloudy days, even those that seem oppressively warm to a person, air temperatures usually remain somewhat below the optimum for the lizards and there is little activity or none at all.

Tolerance of high temperature was tested on July 21, 1951, a sunny day with air temperature 34° C. An adult male collared lizard enclosed in a small wire cone was placed on the ground where he received direct sunlight. Within a few minutes his body temperature (measured rectally with a small thermometer taped in place) had risen to 45° C. and for the half-hour that he was exposed to sunshine, it remained within a degree or two of that level. The lizard showed discomfort by panting and struggling to escape throughout the experiment. He suffered no lasting ill effects, however.

REPRODUCTION

Sexual behavior has been described in many members of the family Iguanidae, including the collared lizard. The general pattern followed is somewhat similar in all members of the group, but there are differences in details. The male approaches the female with "strutting" gait and a display similar to that used to intimidate intruders and to advertise his territorial claim. After display he moves up to the female or about her with a peculiarly relaxed and loose-jointed, slithering gait, with a rapid vibratory nodding of his head (Pl. 6, fig. 2). This behavior differs from that used in meeting or threatening other males. Noble and Bradley (1933: 87) stated that the role of the female in mating was passive but their observations were based largely on lizards in confinement. Evans (1951: 20) emphasized that in the black iguana (*Ctenosaura pectinata*) the female responds by moving nearer to the male and nodding as he does, while in the crested lizard *Leiocephalus carinatus*) the same author noted (1953: 53) that the female might even initiate the courtship with a tail display similar to that of the male. At the height of courtship the iguanid male frequently nips the female or flicks her with his tongue, and the female may reciprocate. It seems likely that olfactory "social releasers" may be brought into play though as a group the iguanids are not especially keen-scented, and the olfactory sense plays a relatively minor role in their lives. Preparatory to actual mating, the male grasps in his jaws loose skin of the female's neck or shoulder and after a pause he thrusts his hindquarters into position beneath the female and effects intromission, which is of only a few seconds duration in some species, and lasts several minutes in some others.

The femoral pores, a linear series of glandlike perforations each in an enlarged scale on the underside of the thigh, have generally been credited with a "hedonic" function. They are present in lizards of several families including most iguanids. They are rudimentary in the female. In the male they produce a waxy exudation which may protrude for a length of several millimeters. The series of protruding exudations are comblike in appearance. In the courting male these structures probably serve for tactile stimulation, as he glides over the female.

Young collared lizards from eggs hatched in August or September may mature sexually early the following summer. If the period of winter dormancy be discounted, the young thus may breed when they are only a few weeks old. This early attainment of sexual maturity together with the species' ability to produce more than one clutch of eggs in a season, gives it a reproductive potential much higher than those of most other North American lizards. These other kinds, both iguanids, and the members of other families, generally have an annual breeding season, and the young produced then remain sexually inactive throughout the following breeding season, and in some, throughout a second breeding season before sexual maturity is finally attained.

In the colony under observation, the advantage conferred by early attainment of sexual maturity was strikingly illustrated. In the spring of 1953 the colony consisted of two old adult females and several half-grown young born late the preceding summer. No adult males were present. Under these conditions it seemed unlikely that any reproduction could occur. However, the half-grown males matured sexually and paired with the females at the usual time, with the result that an abundant crop of young was produced. Approximately two weeks after the young males first mated, a young female had also matured sexually, as shown by the appearance of red "postnuptial" marks laterally. As a result of long conditioning and innate tameness, one old female was indifferent to the presence of persons, even in motion, at distances greater than five to ten feet, and the young male with which she paired was only a little more shy. The series of observations made on this pair, supplemented by less complete observations on several other individuals, as recorded below, serve to illustrate the time relationships of attainment of sexual maturity, courtship, copulation, development of postnuptial colors by the female, and egg-laying.

August 30, 1952. The young male that hatched two or three weeks before, was caught for the last time that summer, and he then had bright scarlet marks on his sides; snout-vent length 53 mm., weight 4 + grams.

May 14, 1953. The young male, caught for the first time after emergence from hibernation, had lateral marks faded to a bright ochraceous; snout-vent length 76 mm., weight 15 grams. He had probably been active as much as eight weeks since the last capture, accounting for his gain of more than 43 per cent in linear dimensions while more than tripling his former weight.

May 28. For the first time the young male was found to be basking beside the female. When they were disturbed by movements of the observer, they tended to keep together or to follow each other in moving off along the ledge. This contrasted with the behavior noted two days earlier when both were on this same part of the ledge, but were at separate basking places several yards apart, with neither displaying interest in the other.

May 29. At 8:20 A. M. the young male was seen basking. The female was emerging five feet away, from a crevice where she had spent the night. After a ten-minute interruption in observations, I found that the female was fully emerged and that the male had mounted her, holding loose skin of her shoulder in a precoital grasp. The female was obviously receptive, as she stood passively or from time to time shifted a few steps. The male maintained his position for approximately ten minutes, fidgeting ineffectually from time to time, frequently releasing his grip to nip at the female's neck and shoulders. He did not succeed in thrusting his hindquarters into position beneath the female, seeming to be handicapped by her much greater bulk (snout-vent length of male 88 mm., of female 100 mm., weight of male 22 gms., of female 44 gms.). For the next hour that the pair was watched, they stayed within a few inches of each other. At irregular intervals for brief periods the male intensively courted the female by moving with the characteristic relaxed slithering gait over and about her, pausing to make rapid nodding movements. He moved in a circular or elliptical course of several inches diameter, around the female's head, flicking her with his tongue, and sliding over her shoulders or body time after time, with frequent reversals of direction. Occasionally the female moved away several inches and twitched her tail in a manner that seemed to catch the male's attention.

May 30. The male had emerged by 8:20 A. M. Five minutes later the female was found to have emerged, and the male already had mounted her and grasped loose skin of her neck. After approximately one minute, he vigorously attempted to copulate and established contact after several seconds. Actual copulation lasted a little less than two minutes. Later the same morning, another young male was seen to copulate with the old adult female that stayed at the east end of the quarry ledge. Late in the afternoon, and again on the following morning, the first male was seen to mount the female and attempt unsuccessfully to copulate.

June 1. The female was watched as she emerged by slow stages from her night's shelter. At 9:27 A. M. the young male, basking on the ledge a few feet away, ran up to her with rapid nodding, and mounted, securing a neck hold. The female's response was a rapid lateral shaking of her head, not seen on previous occasions. The rapid movements seemed to hinder the male in his attempts to maintain the hold, and evidently signified the ending of the female's period of receptivity. For the next eleven minutes the male was on the female's back almost continually, and most of the time was grasping her neck, though this grip was shifted every few seconds. Copulation did not occur, and the male finally gave up the attempt. On this date red marks, though still faint, were appearing on the female's sides.

June 2. The female was again watched emerging from her night's shelter. At 8:55 A. M. when she came into the open to bask, the male approached immediately, and mounted her. The female responded with head shaking, more vigorous than that of the previous day. Clawing the male with her forefeet, she soon discouraged his attempt at courting. Later in the morning, another young male of approximately the same size that had lived on the east side of the ledge near its middle, was found to have crossed over to the west side, probably having been displaced from his usual range by a competitor. I drove him approximately 60 feet farther west along the ledge to the area occupied by the pair under observation. Here he lay flattened against a rock seeking concealment but watching alertly. The resident male had moved still farther west along the ledge to a look-out beyond a clump of vegetation which hid him from view. The intruding young male noticed the female and after watching her for several minutes at a distance of 3 feet, he overcame his initial timidity of the strange surroundings and ran toward her with short, jerky movements. The female responded by standing high with her body flattened dorsoventrally. The male moved up slowly, displaying, and began an intensive courtship, which followed the same pattern as those observed previously. He moved about the female many times in a more or less circular course centering about her head. Frequently he passed over her body or shoulders, with slithering motions, rubbing the undersides of his hindlegs and tail base against her, and occasionally flicking her with his tongue. The female shifted position frequently, and from time to time flicked the male with her tongue. There were pauses when they rested quietly; he usually perched on her back or shoulders. Approximately 20 minutes after the period of courtship began, the male mounted and grasped the female's neck. She was unreceptive and resisted him in the same manner that she had the first young male earlier the same morning. Tipping her head far back, she shook it violently, and progressed with jerky hops obviously calculated to dislodge the male. He clung persistently for the next seven minutes, while the female covered at least 15 feet in an irregular course. Finally when the female paused, he effected intromission, which lasted only about 15 seconds. This young male was never seen subsequently. Probably he was routed when he was discovered by the one already resident on this part of the ledge.

June 3. The female's lateral marks had become bright scarlet. The resident young male noticed her soon after she emerged, and ran up to her, displaying. The female's reaction was strongly negative. She shook her head violently, even before she was grasped by the male, and she stood high off the ground with her body dorsoventrally flattened, making a series of awkward bowing movements with her forequarters. Several times within a few minutes the male mounted and grasped her, and each time she threw him off almost instantly by violent head shaking and by turning on her side, clawing and kicking. She showed no inclination to leave the vicinity or to avoid the male but merely discouraged his attempts at courtship. Soon, he moved away to bask.

On June 3 the other adult female, at the east end of the quarry, had developed dull red lateral spots, approximately one day later than the first female, and four days after observed copulation. These observations indicate that approximately three or four days constitute the normal interval between effective mating and the assumption of postnuptial bright color, with associated physiological change. Shaw (1952:73) reported that a female from Arizona developed postnuptial marks on July 6, two days after observed copulation, but there may have been earlier unobserved mating. This female laid eggs on July 28. Greenberg (1945:229) recorded that a female which mated on April 15 acquired orange spots on April 27. Clark (1946:136) captured a female near Manhattan, Kansas, on May 18, 1946 and kept her alone in a cage. A clutch of eight eggs was found in the cage on June 17 (probably laid on June 15 and 16). A ninth was laid on June 24 and a tenth on June 28. The relatively long time elapsing between copulation and egg-laying in these captive females may have resulted from body temperatures lower than in those maintained under natural conditions where the lizards are able to bask in the sunshine.

I did not attempt to examine nests as the disturbance involved almost certainly would have reduced the success of the hatch. Thorough search at the quarry on June 13 failed to reveal the female that lived on the west part, and she was probably in some concealed situation digging a nest burrow or laying her eggs on that date. On June 15 she was back in her usual place, thin and wrinkled after laying. The other old female was still distended with eggs on that date and had not started her nest burrow, but she was found to have laid on June 19. June 13-14 and June 17-18 seem the most probable laying dates. In each instance laying evidently occurred 16 to 19 days after copulation and 10 to 13 days after scarlet lateral marks had attained maximum brightness. A hatchling almost certainly from the nest of the first female was found on August 4, after an incubation period of approximately 51 to 52 days, and young that must have come from the second nest were taken on August 11, after approximately 54 to 56 days of incubation.

In other years incubation periods were longer. In 1949 one female was known to have laid between June 10 and June 21, and another between June 6 and June 21. The young first appeared on August 19; sixteen were recorded and they were nearly uniform in size. Either they were all from the same clutch or the two clutches hatched at approximately the same time. Possible incubation times ranged from 60 to 74 days.

In 1951 one female was known to have laid between June 30 and July 17, probably near the latter date. Young presumably from this clutch appeared on September 20, after a possible 65 to 82 days of incubation. Another female was known to have laid on July 18, and young that presumably came from this clutch appeared on October 20 after a 94-day incubation period. In 1952 young appeared on August 12, after an incubation period of from 57 to 64 days. In 1954, young appeared on August 19 after an incubation period of from 61 to 64 days.

The relatively long incubation period in 1951 resulted from unusually heavy precipitation and persistently cloudy weather. Air temperature averaged abnormally low, and the soil surrounding the eggs, receiving less than the normal amount of heat by insolation, was even farther below normal. The hatchlings may normally require several days to become active and to escape from the nest cavity, and if this be so, actual incubation periods would be slightly shorter in each instance than those recorded.

Observers at widely separated places in the species' range have noted the appearance of hatchlings in August. Shaw (1952:73) recorded an incubation of 75 days in a clutch laid by a captive female at the San Diego Zoo and artificially incubated at temperatures ranging from 70° F. to 95° F. Presumably the much shorter incubation periods in some of the natural nests resulted from higher average and maximum temperatures. Although the actual nests were not found, they were probably only a few inches beneath the soil surface. Air temperatures may have approximated those recorded by Shaw, but actual temperatures of the eggs during daylight hours probably averaged many degrees higher because soil and rock surfaces over them were receiving direct sunlight.

On July 5, 1954, a typical clear summer day, at 3:15 P. M., when air temperature was 35.5° C., soil temperatures, in Centigrade, on a bank in a spot near a supposed nest site were as follows: At ½ inch depth, 54.0°; 1¼ inches, 42.2°; 2¾ inches, 36.8°; 5½ inches, 32.5°. On the same bank, at a site a few yards away, differing in steepness, direction of exposure, and vegetation, the following temperatures were recorded: 5 inches, 35.2°; 7 inches, 36.3°. It would seem that during incubation the temperature of the eggs often approximates the high levels maintained by the lizards themselves while they are active.

Burt and Hoyle (1934:198) recorded that in a nest found on May 28, 1932, the eggs were loosely packed in moist earth at the end of a short burrow, under a flat rock less than one inch thick and approximately two feet square. The eggs were partly in contact with the underside of the rock, which was exposed to direct sunlight. Burt (1928a:9), on the authority of E. H. Taylor (MS), states that the eggs are deposited at the ends of shallow tunnels immediately below large flat rocks and that the female plugs the entrance with closely packed earth. Strecker found eggs that had been deposited in loose sand at a depth of four or five inches. Having completed the nest, the female devotes no further attention to the eggs or young. Shaw (1952: 73) described eggs laid by a female in captivity as immaculate white, with flexible shells, ranging in length from 18.4 mm. to 20.3 mm. (average 19.14), and in width from 11.4 to 11.7 (average 11.6). Fifty-nine days later these eggs, still 16 days short of hatching, had increased in length on the average 14.73 per cent and in width 32.18 per cent. Force (1930:27) described eggs laid in captivity on June 20, 1926 and July 2, 1928, as of pinkish tint, cylindrical, 21.4 to 25 mm. in length and 10.55 to 13.7 mm. in width. Clark (1946:136) attempted artificial incubation of a clutch of eggs. These averaged approximately 19.9 x 12.5 mm. The eggs became dehydrated even when kept in an atmosphere of 100 per cent relative humidity, and it was necessary to keep at least part of the egg in contact with a moist surface. Oxygen consumption was found to average 77.5 cubic mm. per hour per egg, and average carbon dioxide production was 47.8 cubic mm.

Eggs of the collared lizard number from four to 24 according to Strecker (1910), and several more recent authors. Most clutches probably fall within this range, but the specific records available to me indicate that there are seldom more than twelve eggs, and that occasionally there may be fewer than four. For 29 clutches (12 recorded in the literature and 17 others observed by me) the numbers ranged from 2 to 21 with an average of 7.55 ± .70 per clutch. Of the 29 clutches, 19 pertain to Kansas; the remaining ten were from females from Missouri, Texas, New Mexico, Arizona, and California. Most of the figures pertain to unlaid eggs found in females dissected, or to clutches laid in captivity. The sources of published information and numbers of eggs recorded are: Anderson (1942: 207), 8; Burt (1928: 10), 7 and 9; Burt and Hoyle (1934: 198), 16; Clark (1946: 136), 10; Ditmars (1915:113), 21; Greenberg (1945: 229), 8, 6, and 6; Hallowell (1856:239), 8; Johnson, Bryant and Miller (1948: 259), 2; and Shaw (1952: 73), 7.

On June 17, 1951, I collected nine females four miles southwest of Garnett, Anderson County, Kansas, five of which had large uterine eggs 21 to 22½ mm. in length and 11½ to 12½ mm. in width. Three others had recently laid their clutches as shown by the enlarged and collapsed condition of the uteri, with conspicuous corpora lutei, and the remaining female had enlarged ovarian eggs. One had twelve eggs, two had 7, one had 6, four had 5 and one had 3. For the four largest females of this group (snout-vent lengths 97 to 102 mm.) clutches averaged 7.5, while for the five smallest (snout-vent lengths 83 to 93 mm.), clutches averaged 5.0. Other clutches from Kansas include two each with 6 eggs, from Coffey County, three with 10, 8, and 8 eggs from Wabaunsee County, and one with ten eggs from Anderson County. A female brought from Coconino County, Arizona, (Pl. 4, fig. 2), laid a clutch of four eggs. One from Guadalupe County, New Mexico, contained 5 eggs.

Large old females on the average produce larger clutches than females that are laying for the first time, and are not yet full-grown. Although no counts were obtained of the clutches laid at the quarry, the greater productivity of the older and larger females was shown by their much greater weight loss at the time of laying. Females containing eggs that are mature or nearly mature are of plump and distended appearance. The thin and wrinkled appearance of females that had recently laid was also characteristic. The weight loss amounted to as much as 45 per cent.

The incidence of casualties in the eggs must have been high. Over six seasons known clutches were distributed as follows: Two in 1949, producing 16 young; one in 1950, producing one young; two in 1951, producing six young; two in 1952, producing eight young; four in 1953, producing 12 young; and one in 1954 producing five young. For the six-year period the twelve known clutches thus produced a known total of 48 young, an average of four per clutch. Several of the clutches known to have been laid were seemingly not represented by any of the young and must have been entirely destroyed by predators or unfavorable weather. The number of young actually hatched doubtless exceeded the number recorded, as some were not caught until they were several weeks old, and at that age their numbers must have been already much reduced by various mortality factors. The actual hatch probably averaged at least five per clutch.

Except for the anoles, which produce only one egg at a time, iguanids have not been known to produce more than one clutch per season. However, in 1953, a collared lizard at the quarry laid two clutches of eggs. Her first clutch was laid sometime between June 8 and June 15, and the second on July 5. A first-year female produced her clutch between July 6 and July 9. Late hatching clutches thus might be either the second clutches of old adults, or the first clutches of young females that bred later because of their immaturity. Of the 12 known clutches produced at the quarry only the one was a second clutch of the season. Otherwise I have no basis for judging the frequency of second clutches. My observations were made at the northern edge of the species' range where the growing season is of minimum length. Second clutches might be of more frequent occurrence farther south. As the production of a second clutch soon after the first was entirely unexpected, other instances may have been overlooked. Most of the females were not caught frequently enough to establish conclusively that they produced no second clutches. I suspect that second clutches are produced only by females that are fully mature, where there is an abundant food supply, and other environmental conditions are exceptionally favorable. Even more important in the time of appearance of hatchlings is the weather before and during the breeding season.

GROWTH

The relatively rapid growth of the collared lizard is remarkable. This lizard is larger than many other lizards that have a growing season just as long and require much longer to attain adult size and sexual maturity. Growth is most rapid during the first week of life, when the daily increment in snout-vent length seems to exceed 1 mm. At first, egg yolk retained in the body cavity after hatching supplements the voracious feeding of the young. Nearly all of the young captured were well above hatching size when first recorded, although they could not have been more than a few days old. One young marked while still near the minimum size at a length of 42 mm. had grown to 53 mm. 13 days later; another marked at a length of 41 mm. had grown to 48 mm. seven days later; a third, marked at 41 mm. had grown to 49½ mm. nine days later. For these three individuals, which provide the best records of early growth, the rate averaged a little less than 1 mm. per day, but probably growth was more rapid during the first few days than

TABLE 2.—BREEDING RECORDS OF FEMALES.

Toe formula of individual and year of birth	Year	Earliest record after hibernation	Period within which "postnuptial" red marks appeared	Period within which laying occurred	Weight in grams	
					Before laying	After laying
1x2x before 1948	1949	not recorded	May	June 10–21	63	48
1x4x before 1948	1949	not recorded	early June	June 6–21	42	25
15xx 1948	1950	April 26	not recorded	June 15–July 6	44.9	28.8
2x1x 1949	1951	May 12	June 16–19	July 17–19	35	22
25xx 1949	1950	April 26	did not breed			
	1951	May 28	did not breed			
	1952	May 7	June 1–16	June 16–July 1	39	27
	1953	May 19	June 3–8	June 15–19	47	32
	1954	April 26	May 23			
2x4x 1949	1950	May 9	did not breed			
	1951	May 20	May 30–June 9	June 30–July 17	42	26
	1952	May 5	May 25–28	June 9–16	40	27
	1953	May 21	June 1	June 8–15	49	28.3
				July 4	44	24
	1954	April 24	May 27–June 9	June 18–21	47	31
xx4x 1952	1953	May 29	June 17	July 6–9	28	20

TABLE 3.—GROWTH RATES UNDER NATURAL CONDITIONS IN YOUNG COLLARED LIZARDS OF FOUR DIFFERENT SIZE GROUPS.

Mean snout-vent length of lizards at beginning and end of sampling periods	Number of lizards in sample	Mean increment in snout-vent length per day in mm.
42.6—52.9	8	.71
59.7—69.5	45	.52
74.9—79.5	15	.30
82.3—85.1	7	.20

it was later. The slowing trend of growth with larger size is brought out by Table 3.

At the time of hatching, and in the early stages of growth males and females are of similar size. As growth proceeds however, the males become noticeably larger than females of the same age, and this tendency is more pronounced in the later stages of growth. The following table shows difference in growth rate at middle and late stages in the process of growth.

TABLE 4.—COMPARISON OF GROWTH RATES IN MALES AND FEMALES OF SIMILAR SIZE AT TWO DIFFERENT STAGES IN DEVELOPMENT.

Size group	Males			Females		
	Mean snout-vent length	Number in sample	Mean increment, mm. per day, snout-vent length	Mean snout-vent length	Number in sample	Mean increment, mm. per day, snout-vent length
Smaller	63.95	21	.531	62.1	19	.426
Larger	88.08	9	.281	86.2	8	.226

In females, growth slows abruptly at a snout-vent length of 90-95 mm., and females usually breed for the first time while they are within this size range. Adult males average several millimeters longer than females.

In Table 5 some selected records are presented for several of the individuals, showing the trend of increase in snout-vent length, tail length and weight, from hatchling to maturity and, in some instances, to an age of several years. Continued gradual increase in size in the adults is shown. Weight was recorded on a balance accurate to 0.1 gram in those brought to the laboratory, but more frequently

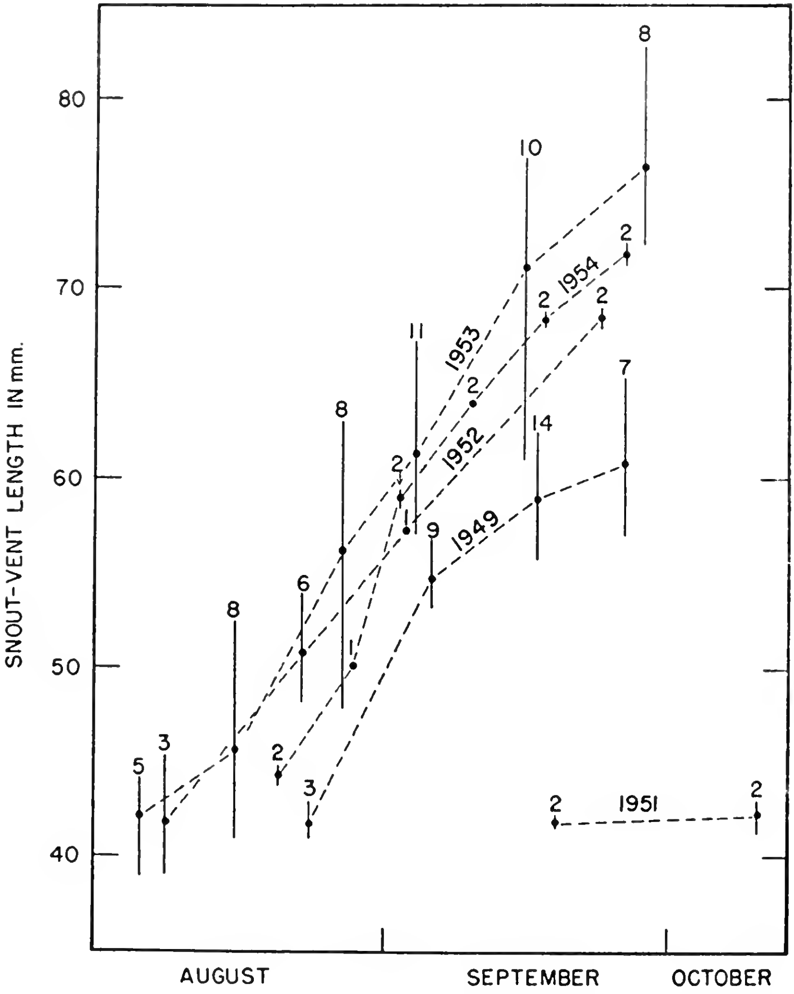


FIG. 4. Average snout-vent length in young collared lizards grouped in ten-day intervals, from the time of hatching until retirement into hibernation. During this time growth is rapid but the average size on any given date varies from year to year, depending largely on the weather.

lizards were weighed in the field with a spring scale having a margin of error of approximately one gram. Weights having no decimals are those recorded with this spring scale.

Hatchlings have a two toned pattern of dark brown and yellowish tan (Pl. 2, fig. 1). On the body there are five narrow transverse bands of the paler color. Between these bands the interspaces are nearly twice as wide, and they have numerous small rounded spots of the darker color separated by narrow areas of the paler color in a reticulate arrangement. The spots nearest the middorsal line are the largest and most distinct. Farther laterally the spots become progressively smaller and less distinct, with outlines blurred, and they fade into the immaculate white of the ventral surface. Irregular transverse marks and small spots of the darker color are present on the dorsal side of the tail, thigh, and lower leg, and on the side of the face. The collar is well developed. The bright colors of adults, green, yellow, orange, and scarlet, are lacking.

As growth proceeds, the original banded pattern becomes obscure (Pl. 5, fig. 2). The dark spots enlarge and fuse, encroaching on the transverse bands which become faint and broken. These changes proceed more rapidly in males than in females. In males that are still far short of adult size, as well as in adult males and old adult females, the original banded pattern is no longer evident. In young males, even as early as a week after hatching, a series of bright spots, irregular in size and distribution, appear on both sides of the body and neck. These spots are ochraceous at first, but within a few days they brighten to orange and finally to scarlet. These bright lateral spots have been seen in young chiefly in the months of August, September, April and May. At a snout-vent length of 80 mm. or a little less, the scarlet marks fade and disappear with relative suddenness in the course of a few days.

In a young male approximately seven weeks old when he was examined on September 18, 1952, the scarlet marks had reached approximately their maximum development. In other respects the pattern was transitional between those of hatchlings and adults, but more like the latter. The over-all dorsal ground color was dull brown with the transverse marks only faintly discernible. As in adults the dorsal surface was dotted with white.

TABLE 5.—GROWTH AND DEVELOPMENT IN INDIVIDUAL MALES.

Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.				
Aug. 20, 1949	42	62	....	Probably not more than 3 days old.
Sept. 21, 1949	65	105	12.1	
June 13, 1950	83	143	20.5	
July 8, 1950	89	152	25.5	
July 24, 1950	91	159	28.2	
Aug. 24, 1950	98½	171	39.1	One year old and nearly full-grown.
Sept. 8, 1950	100	173	43.5	
May 20, 1951	104	176	38	
July 17, 1951	106	182	44	
Aug. 10, 1951	107	186	46	
May 25, 1952	107	189	42	Near maximum adult size at 33 months.
No. 2.				
May 10, 1952	58	95	7	Hatched late Sept. or Oct. 1951. Has scarlet spots.
May 28, 1952	65	107	8	
June 21, 1952	68	108	9.3	In captivity June 2–July 2. No growth during this time.
Aug. 12, 1952	92	165	18.7	Scarlet marks gone; has adult male pattern.
Aug. 29, 1952	96	171	33	Almost full-grown at approximately 11 months.
July 16, 1953	102	184	38	Near average adult male size.
No. 3.				
Aug. 22, 1952	50	78	4.0	Probably 10–12 days old.
Aug. 29, 1952	53	84	....	Scarlet spots have become prominent.
May 14, 1953	76	124	15	Spots dulled to ochraceous.
May 26, 1953	81	137	22	Spots no longer evident; adult pattern.
June 2, 1953	84	142	22	
June 16, 1953	93	162	27	
July 3, 1953	96	173	32	
July 16, 1953	100	182	33	
July 29, 1953	103	187	42	
Aug. 11, 1953	106	191	44	Grown to large adult size at age of one year.
April 18, 1954	105	193	45	
No. 4.				
May 30, 1953	86	149	23.4	Perhaps brood-mate of No. 3; avoided capture previously.
June 8, 1953	88	153	25	
June 26, 1953	95	170	30	
July 9, 1953	99	180	30	
July 25, 1953	103	184	39	Grown to adult size at 11½ months.
April 24, 1954	104	190	47	
May 18, 1954	106	197	43	
June 11, 1954	105	196	43	

TABLE 6.—GROWTH AND DEVELOPMENT IN INDIVIDUAL FEMALES.

Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 1.				
Sept. 9, 1949	55	85	....	Approximately three weeks old.
May 24, 1950	67	103	10.4	
June 10, 1950	72	111	....	
June 19, 1950	76	119	15.7	
July 11, 1950	84	132	19.5	Had not attained sexual maturity.
Aug. 14, 1950	88	142	25.0	
May 20, 1951	93	128	28	Tail tip missing.
Aug. 30, 1951	95	133	31	Tail tip missing. Scarlet marks faint; appeared June 16.
No. 2.				
Sept. 9, 1949	55	88½	7.5	Approximately three weeks old.
Sept, 16, 1949	59	92	7.7	
April 26, 1950	60	98	8.4	Newly emerged from hibernation.
May 24, 1950	69	114	11.8	
June 19, 1950	77	130	17.3	
July 6, 1950	86	143	22.1	Slightly retarded; not breeding.
Aug. 5, 1950	90	156	25.2	
Sept. 1, 1950	94	158	30.5	
May 29, 1951	93	161	27	
Aug. 30, 1951	96	168	34	Failed to breed in 1951; 10 captures, June, July, Aug.
May 25, 1952	97	170	27	
July 1, 1952	100	173	27	Postnuptial markings; laid first clutch since June 16.
Aug. 13, 1952	100	173	37	Scarlet marks much faded.
May 19, 1953	100	173	42	Recently emerged from hibernation.
July 16, 1953	101	178	38	Scarlet marks becoming dull; had laid in mid-June.
June 9, 1954	102	176	44	Gravid; caught by hawk on June 20.
No. 3.				
Sept. 18, 1949	60½	93	8.5	Approximately one month old.
May 9, 1950	64	99	10.0	Hibernating most of time since Sept. 18.
June 15, 1950	79	128	17.3	
Aug. 5, 1950	89½	151	22.9	Growth somewhat retarded; had failed to breed.
Sept. 1, 1950	94	154	30.3	
May 30, 1951	96	159	34	Breeding; had developed red marks by June 9.
Aug. 18, 1951	97	163	35	Red marks retained until end of month.
May 5, 1952	97	163	32	Recently emerged from hibernation, smeared with mud.
July 10, 1952	100	169	39	
July 6, 1953	102	172	24	Had just laid eggs, the 2nd clutch for 1953.
April 24, 1954	103	172	40	Grown to large size for female; last recorded June 23.

TABLE 6.—GROWTH AND DEVELOPMENT IN INDIVIDUAL FEMALES.—(*Concluded*)

Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
No. 4.				
May 29, 1953	76	133	15.1	Must have hatched in early Aug. 1952.
June 15, 1953	84	144	23.2	Maturing sexually, postnuptial spots developed June 17.
July 9, 1953	87	152	20	Had laid eggs recently.
Aug. 9, 1953	95	168	28	Rapid growing has continued.
May 13, 1954	96	170	33	Near average female size at 21 months.

Fig. 5 shows the time of appearance, duration, and disappearance of the red marks in a group of young males. At about the time the red spots are suppressed usually at a snout-vent length of approximately 80 mm., the dorsal surface begins to take on the greenish tint characteristic of adult males. The young males are then readily distinguishable from females of the same age, which retain the dull tones of the hatchlings.

REGENERATION AND RECOVERY FROM INJURY

The collared lizard differs from many iguanids and from lizards of other families also, in having a less fragile tail. In some kinds of lizards the tail is broken and regenerated repeatedly in the individual's lifetime, and an adult retaining the original tail intact is a rarity. In the collared lizard, however, the tail is rarely broken. Of the 61 individuals studied at the quarry, only two suffered injuries to their tails, each losing only the tip. There was no regeneration in either. In handling the lizards, I often held them by the tails near the base, and they never broke their tails nor tried to do so. I have not examined extensive series to determine the incidence or extent of regeneration. Proportions of the tail change during ontogeny. In a series of ten young within a few millimeters of hatching size, tail length averaged 145.2 (151 to 139) per cent of the snout-vent length. In six adult females tails averaged 171.3 (178 to 162) per cent of snout-vent length, and in eight adult males tails averaged 178.6 (183 to 174) per cent of snout-vent length.

On June 2, 1952, in catching by hand a young male having a snout-vent length of 68 mm., I broke his right thigh. As there seemed to be little likelihood of his surviving this injury under natural conditions, and as the colony was then at low ebb, I kept this lizard in the laboratory, taped his leg with a crude splint, and force fed him with grasshoppers. After 19 days the leg seemed to

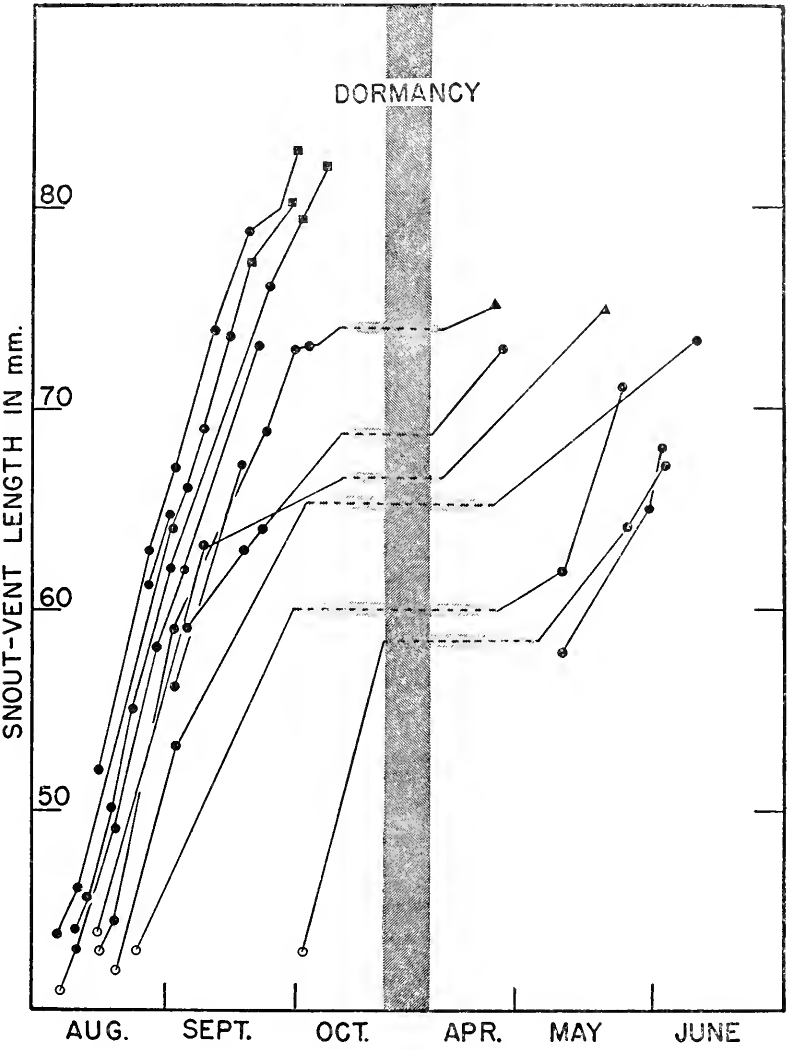


Fig. 5. Growth and stages of pattern change in individual juvenal males. Dots indicate presence of scarlet lateral spots, open circles indicate that these spots had not yet been acquired, and squares indicate that these spots had faded or disappeared. A few records, those marked with triangles represent intermediate stages in which the spots are fading but still discernible. Winter dormancy is of varying duration, as several different years are represented by the individuals included.

be nearly healed. After a month the lizard was released and was able to run normally. In the month of his captivity his length and weight remained static, but in the 41 days after he was released he doubled in bulk with corresponding increase (24 mm.) in snout-vent length.

MOLT

Like most other reptiles, collared lizards periodically slough the outer layer of dead epidermis. The molt follows a characteristic pattern which varies but little among individuals. The disposition and daily routine of the individual is but little affected by molt. In keeping with the xeric habitat, the lizard loses but little moisture in the process of molt. Moisture is scarcely perceptible on the underside of a patch of skin that is in process of being shed.

In a young collared lizard captured and observed in the process of molt on June 4, 1952, several major splits in the old skin were noted, one along the mid-dorsal line on the body, from the shoulders to the root of the tail, one transversely across the rostrum, another across the base of the tail, and one along the side of the head above the supralabials. The molt is relatively rapid. It begins with peeling back of the old skin in the labial region, which may occur on the day before the remainder of the skin is shed. Most of the molt takes place within a few hours, however. For instance on the afternoon of July 24, 1951, an adult male was caught and examined twice within an hour. At the first capture the molt was not noticeably underway, but at the second capture most of the old skin had been sloughed off. The outer layers of dead epidermis that loosen and peel off are transluscent with the pattern faintly discernible. The forelegs become free of the old skin first. On the body, skin adheres longest to the middle of the belly.

Remarkably little is known concerning the frequency of molt in reptiles living under natural conditions. In an effort to determine the frequency of molt, I marked the chin of each lizard with indelible black ink each time it was captured. In those lizards found to have lost the ink marks, it could usually be assumed that one or more molts had occurred since the last capture. Although the record of molts is not complete for any one individual, the records are sufficiently numerous and continuous to reveal the general trends. Molt is most frequent in small young that are in their period of most rapid growth, from the time of hatching until the first hibernation. Six young, each of which was caught soon after hatching and frequently thereafter up to the time of hibernation, best illustrate frequency of molt at this stage of development. One had molted twice in 34 days when last captured on September 19. Each of two others had molted three times when last captured on September 19 and September 23. Each of three others had molted four times when last captured on September 30 (one) and October 3 (two).

Unlike many other lizards and most snakes, collared lizards seem not to have a postnatal molt. From the snout-vent length at hatching of 40 mm. or a little more, up to 52 mm., none of the six young mentioned above had undergone its first molt. Those caught in the period between the first and second molts were all in the size range 53-67 mm., between second and third molts, 66-74 mm., between third and fourth molts, 72-82 mm., and those that had molted a fourth time, 76-83 mm., thus having approximately doubled their linear dimensions and increased to at least eight times their original bulk.

Following emergence from their first hibernation, the young continue to grow rapidly, and attain a size near that of adults by the end of this first full growing season. Within this growing season they molt at least four times, and probably five molts are more typical. In seven instances individuals were caught while in the process of molt on two successive occasions, and the interval ranged from 15 to 27 days, averaging 23 days.

In those lizards that have attained adult size after two or more hibernations, frequency of molt is only a little reduced, and five molts per growing season still seems to be the usual number. In five instances individuals were caught while in the process of molt on two successive occasions and the interval ranged from 16 to 38 days, averaging 25.4 days. No difference in frequency of molt was evident between the sexes, either in young or in adults.

NUMBERS

There are no statements in the literature concerning the population density of collared lizards under natural conditions. Klauber (1939: 80) mentions the unusual abundance of these lizards in an area of scattered boulders south of Ashfork, Arizona, and Burt (1927: 3) mentions their abundance in rock-ledge areas of Riley County, Kansas.

The original lot of ten collared lizards released on the Reservation at the old quarry site in early May, 1949, consisted of a large old adult female, an adult female of approximately average size, and eight young, presumably all of the 1948 brood, although some were already approaching adult size. By the end of May, 1949, two of these young were eliminated, and others in turn disappeared until by mid-August of 1951 none of the original group remained. However, they had been replaced by young of the three successive annual broods. In the years 1949 to 1954 inclusive, the population fluctuated continually, reaching a minimum of one in July, 1954, and a maximum of 23 in August, 1953. During most of the time the population consisted largely of individuals short of adult size and sexual maturity. Those that were fully adult were usually in the minority. Excluding those that were less than a year old, the adults present throughout the six-year period of the study varied from two to six. Invariably when only two adults were present both were females. There were never more than two adult males present at any one time, and for part of each year only one was present or none at all. When two adult males were present, they divided the ledge between them, one on the west half and one on the east. Continuity of the rock outcrop was broken by an old road crossing it near the middle, and this division was generally respected as a territorial boundary. When only one adult male was present, as in August 1950, September 1951, May and June 1952, and May, June and July 1953, he usually ranged freely over the entire area of the quarry. Maximum numbers were attained in late August or September, after the annual brood of young had hatched.

At most times the population of the area consisted of from five to nine individuals which seemed to constitute the carrying capacity of the available habitat. Successful hatches in 1949, 1952 and 1953 resulted in temporary expansions of this small population, but in each instance the excess individuals were rapidly eliminated.

The high incidence of mortality from month to month in the first year of life is brought out by Table 8.

For hatchlings appearing in August the chances of surviving into September were good. However, many did not appear until late August, so that the average time involved from hatching until a capture in September, was considerably less than a month. More than one-third of the young present in September were eliminated by the following May, but these casualties include losses in the hibernation period as well as losses in the season of activity including for some, parts of October and April. Of the survivors nearly one-third were eliminated from May to June but the heaviest losses, nearly half, were sustained in the June to July period. At this stage young were maturing sexually, and increasing territorial

TABLE 7.—NUMBERS OF COLLARED LIZARDS OF EACH SEX AND AGE GROUP PRESENT IN EACH MONTH OF THE STUDY.

Month	Total	Adults	Yearlings	Hatchlings
May 1949	9	2(both ♀♀)	7(4♂♂, 3♀♀)	
June 1949	8	2(both ♀♀)	6(3♂♂, 3♀♀)	
July 1949	6	2(both ♀♀)	4(3♂♂, 1♀)	
Aug. 1949	8	2(both ♀♀)	3(2♂♂, 1♀)	3
Sept. 1949	20	1(♀)	3(2♂♂, 1♀)	16
May 1950	19	4(3rd yr ♀, 2nd yr ♀, 2 2nd yr ♂♂)	15	
June 1950	12	4(2 2nd yr ♂♂, 1 3rd yr ♀, 1 2nd yr ♀)	8(2♂♂, 6♀♀)	
July 1950	8	3(2 2nd yr ♂♂, 1 2nd yr ♀)	5(1♂, 4♀♀)	
Aug. 1950	8	3(2 2nd yr ♂♂, 1 2nd yr ♀)	5(1♂, 4♀♀)	
May 1951	7	6(1 3rd yr ♂, 1 3rd yr ♀, 1 2nd yr ♂, 3 2nd yr ♀♀)	1(♂)	
June 1951	7	6(as above)	1(♂)	
July 1951	5	5(1 3rd yr ♂, 1 2nd yr ♂, 3 2nd yr ♀♀)		
Aug. 1951	5	5(as above)		
Sept. 1951	9	4(1 2nd yr ♂, 3 2nd yr ♀♀)		5(2♂♂, 3♀♀)
May 1952	5	3(1 3rd yr ♂, 2 3rd yr ♀♀)	2(♂♂)	
June 1952	5	3(as above)	2(♂♂)	
July 1952	4	2(3rd yr ♀♀)	2(♂♂)	
Aug. 1952	12	2(3rd yr ♀♀)	2(♂♂)	8(5♂♂, 2♀♀, 1 unidentified)
Sept. 1952	9	2(3rd year ♀♀)	2(♂♂)	5(4♂♂, 1♀)
May 1953	9	3(2 4th yr ♀♀, 1 2nd yr ♂)	6(4♂♂, 2♀♀)	
June 1953	8	3(as above)	5(4♂♂, 1♀)	
July 1953	7	3(as above)	4(3♂♂, 1♀)	
Aug. 1953	23	3(as above)	3(2♂♂, 1♀)	17(8♂♂, 9♀♀)
Sept. 1953	21	3(as above)	3(2♂♂, 1♀)	15(8♂♂, 7♀♀)
May 1954	11	5(2 5th yr ♀♀, 2 2nd yr ♂♂, 1 2nd yr ♀)	6(4♂♂, 2♀♀)	
June 1954	6	4(2 5th yr ♀♀, 2 2nd yr ♂♂)	2(♀♀)	
July 1954	1	1(2nd yr ♂)		
Aug. 1954	6	1(2nd yr ♂)		5

pressure probably accounts for the high incidence of casualties. Those surviving this critical period lived in much greater security from July to August and August to September. By then they were either fully mature or near adult size.

Of twelve adults that were eliminated from the quarry area over the entire period of the study, times of disappearance were as follows: September to May, 2; May to June, 1; June to July, 6; July to August, 2; August to September, 1. Evidently the June to July period is the most hazardous. Of the six eliminated in this period, four were females. The females are perhaps especially vulnerable to predation just before laying, when they are heavy with eggs, and in the process of digging a nest burrow and laying, when they venture farther than usual from their accustomed escape shelters. Nevertheless, females seemed to have a longer life expectancy than males. Six females that were already a year old survived beyond this age for periods of 46, 46, 34, 22, 13 and 1 months, respectively, for an average of 27 months. The six males that lived to be a year old survived beyond this age for periods of 24, 22, 12, 11, 2 and 1 months, an average of only 12 months. Territorial pressure among the males probably accounts for their relatively high rate of mortality. Presumably in natural populations of collared lizards, adult females usually outnumber adult males, although the latter are more often seen by the casual observer because of their brighter colors and conspicuous territorial perches.

TABLE 8.—MONTH-TO-MONTH INCIDENCE OF CASUALTIES IN YOUNG COLLARED LIZARDS FROM THE TIME OF HATCHING.

	August to September	September to May	May to June	June to July	July to August	August to September
Number in sample	25	40	36	26	15	12
Percentage of casualties	12	37	31	46	7	14

TERRITORIALITY

Intraspecific combat, especially that between breeding males, has been described in many kinds of reptiles, but well defined territoriality has been demonstrated in relatively few. The cosmopolitan geckonids and the Old World agamids have some members at least that are territorial. In North America, however, territoriality has been demonstrated chiefly in members of the family Iguanidae. Social behavior, either under natural conditions or in captivity, has been studied in detail in several members of this group. Behavior patterns characteristic of the family as a whole, and similarities and differences between genera, and between species in the same genus have been demonstrated.

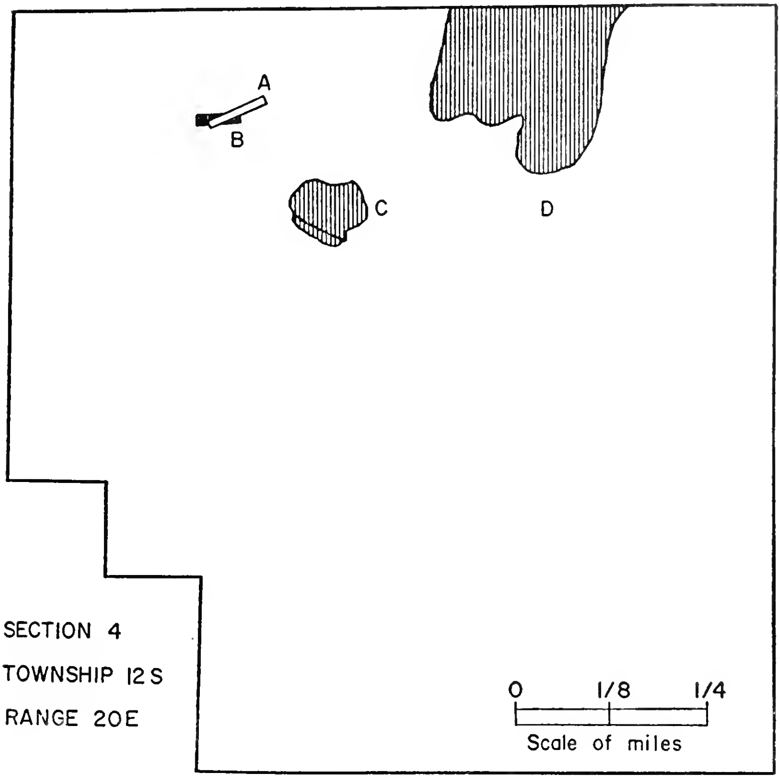


FIG. 6. Map of University of Kansas Natural History Reservation, the section of land in the northeastern corner of Douglas County, approximately five miles north northeast of Lawrence.
A. Location of study area at quarry shown in Figs. 8 and 9.
B. Location of west part of quarry area shown in detail in Fig. 7.
C. Location of pond deepened in 1954.
D. Location of eroded hilltop field sown with seeds of native grasses in 1949.

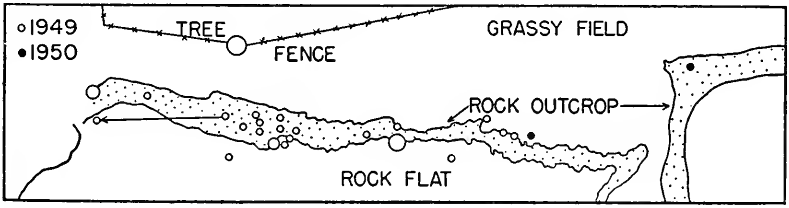
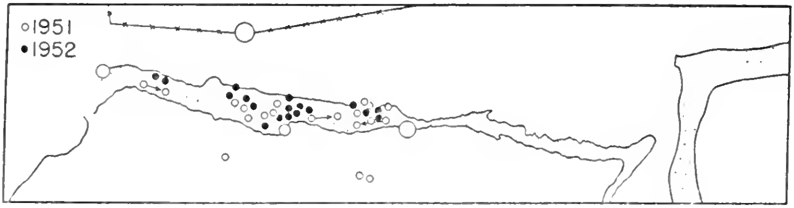
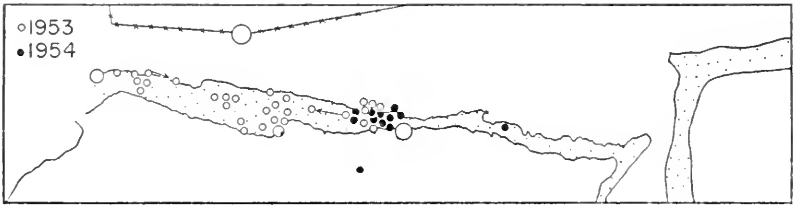


FIG. 7. Map of west part of the quarry showing locations of capture of a female (2 x 4 x), in late summer of 1949 as a hatchling, and in 1950 as a juvenile and subadult; larger circles represent bushes or small trees.



(b) Locations of capture of the same female in 1951 and 1952 as an adult.



(c) Locations of capture of same female in 1953 and 1954 as an adult.

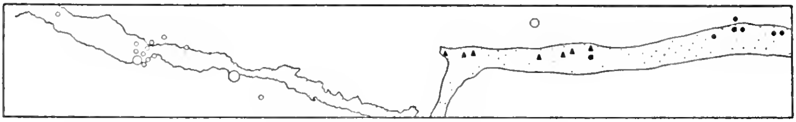


FIG. 8. Map of the quarry area with locations of capture in August 1950 of the four females present then (each represented by a different symbol, small circle, triangle, square, and dot, respectively). Areas occupied by these individuals were largely complementary with only slight overlapping.

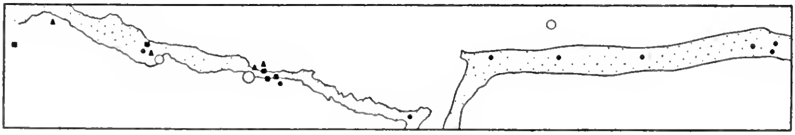


FIG. 9. Same area shown in Fig. 8, with locations of capture in August 1950 of the three males present then. The areas of the two adults were mainly complementary, but one (dot) being dominant, encroached on the area occupied by the other (square). The third, not yet fully grown, was tolerated by both adults and stayed in the territory of the second. Territories of males were larger than those of females and overlapped them.

The display of the male has been noted by many observers to be similar in both combat and courtship. In most iguanids the male is larger and more brightly colored than the female. Conspicuously colored areas, gular pouch in the anole, ventrolateral blue patches in the fence lizard, undersurface of the tail in *Leiocephalus carinatus,* inside of the mouth in the black iguana, are prominently displayed to an adversary before actual combat, and also as a substitute for combat, which serves to intimidate the rival. In territorial defense, it is characteristic that the male's colors brighten and his body is dorsoventrally flattened as he stands high off the ground and performs bobbing movements which render him more conspicuous.

The anoles (*Anolis carolinensis* and *A. sagrei*) have been most thoroughly studied. Evans (1936) found that in confinement males of *A. carolinensis* arranged themselves in a hierarchy of dominance with the largest and most vigorous individual at the top of the scale. Oliver (1948: 26) and Evans (1938: 123) both made field studies on populations of *A. sagrei* and found that the adult males normally occupy territories that are mutually exclusive, but the territory of the male may be occupied by several adult females and by immature individuals of both sexes.

Evans (1951) studied a concentrated population of the black iguana (*Ctenosaura pectinata*) inhabiting a stone wall near a cultivated field that provided an abundant food supply. He found that the entire colony was dominated by a "tyrant," a large adult male that roamed at will over the area, enforcing his "right of trespass" by intimidating displays and perhaps by actual attacks. The other adult males were spaced along the wall, occupying relatively small and mutually exclusive territories, but with some indication of a scale of dominance among them. Many subordinate individuals, females and young, also lived in this wall without defending the areas they occupied. Evans observed that in more typical habitat away from the cultivated areas offering a concentrated food supply, black iguanas were solitary, each presumably defending its territory against all others.

Schmidt (1935: 72) studied the marine iguana (*Amblyrhynchus cristatus*) at Narborough Island of the Galapagos group, and found that adult males tended to be regularly spaced at intervals of five to ten feet along the ocean shore, each defending his narrow strip against other adult males. Occasionally adjacent males would fight by butting with their knobbed, horny foreheads. Females and young were massed higher on the beach, and each male dominated the group within his area.

Social behavior has been studied in several species of the scaly lizards, *Sceloporus*, by Newman and Patterson (1909, *S. olivaceus*), Noble (1934, *S. undulatus*), Fitch (1940, *S. occidentalis*), and

Stebbins and Robinson (1946, S. *graciosus*), and Evans (1946, S. *grammicus*). Although numerous specific differences are evident the general pattern is similar in all. The males generally occupy and defend separate territories except where there is overcrowding in a situation providing ample food and shelter for several individuals. Under such conditions several may be co-occupants of the same small area, and one dominates the others, which tend to arrange themselves in a scale of dominance. Males defend their chosen areas with combat, pursuit, and bobbing displays, in which the brilliantly colored throat and ventrolateral body patches are shown to advantage. A female may stay in association with a male but does not participate in defense of the territory.

Evans (1953) studied a group of *Leiocephalus* in captivity and found that one male was dominant, his displays and aggressive behavior inhibiting others. When he was removed, other adult males competed for his dominant position, and there was indication of a scale of dominance, upset by removal of the top-ranking individual. Females showed no aggressive behavior.

Greenberg (1945) studied a group of collared lizards under laboratory conditions and their social behavior was in some respects remarkably similar to that of the *Leiocephalus* studied by Evans. The females were passive in behavior. One male dominated the others, and for the most part inhibited their aggressive behavior. When this top-ranking individual was removed, another in turn took over his dominant position. When the group was subdivided into several smaller groups, each was dominated by the most vigorous male. The orange throat of the male was noted to serve for sex recognition, and when in view, it elicited a fighting response on the part of other males. In describing combat behavior Greenberg stated that "The fighting male assumes a posture that appears to be characteristic for iguanid lizards. . . . The throat is puffed up so that the yellow-orange coloration shows clearly, and the body is laterally compressed. Stiff and deliberate bobbing movements are performed, the male rising higher and higher in jerky fashion. Since the hind legs are larger than the front legs, the male may rise until only the tips of the fingers still touch the substrate. . . . and he then flings himself at the opponent with great speed. . . ."

In the course of my study I saw several dozen instances of aggressive behavior which were interpreted as territorial defense. Ordinarily individuals avoid attack by keeping within their own territories, which others tend to respect. Posturing and display may serve to establish, or at least to maintain, the territorial claim without resort to outright combat. The characteristic postures and responses described by Greenberg were observed under natural conditions. However, the social life of these free-living lizards was organized along much different lines than in those crowded together in confinement. Each individual tends to stay in a relatively small area that is familiar to it. However, defense of this area as a territory is not absolute. Territorial boundaries are vaguely defined, and are continually shifting. The open type of habitat preferred by this lizard permits an individual to see any others within a radius of many yards. Such perception is facilitated by the lizard's use of elevated perches, from which it surveys its surroundings. Eyesight is well developed.

The well developed territoriality of the male is accompanied by marked sexual dimorphism. Various authors have commented on the male's wider head, with enlarged muscles in the temporal region, swollen tail base (lodging the hemipenes), enlarged postanal scales, and enlarged femoral pores. More conspicuous differences are to be seen in the color pattern. The female retains in part the juvenal pattern, altered chiefly by a blurring of the markings, which are sharply defined in the young. In the adult male, however, the juvenal markings are completely lost, and bright colors are acquired, rendering him conspicuous from a distance. These distinctive bright colors serve to advertise sex and territorial claim. Stereotyped behavior patterns are associated with these colors, serving to display them to best advantage. The dorsal pattern is bright green with numerous small white spots. The head may be of duller color, but in one population, *C. c. auriceps*, of eastern Utah, the head is bright yellow. Along the sides of the body the green is intensified to a deep blue-green. Most of this highly colored ventrolateral area is largely concealed when the lizard is at rest, but is brought into prominence when the lizard stands erect with body dorsoventrally flattened to display. The skin of the throat is distensible into a gular pouch, likewise conspicuous from lateral view and used in display. An adult male stimulated by the appearance of another collared lizard, either adversary or possible mate, shows behavior calculated to display to best advantage the bright colors that are normally hidden.

Of the nine individuals present at the quarry in late May, 1949, four were males, probably all young of the previous summer. One had a mangled hind foot, probably injured in fighting, and this individual had disappeared by the end of May. Another was last seen in late July when he had grown nearly to adult size. The remaining two survived as co-occupants of the quarry for more than a year afterward. One of these was noticeably smaller, and the larger one tended to dominate him. The smaller one ordinarily kept to the west half of the ledge. He was recorded on the east part only once. The larger one shifted frequently, and at various times occupied all parts of the ledge. From time to time he moved his activities into the area usually occupied by the smaller, either displacing the latter completely, or forcing him to desert his favorite look-outs and to stay in concealment.

On August 20, 1950, this larger male had moved into the smaller one's territory and was on one of the smaller's favorite basking sites, probably after a decisive encounter between the two. The smaller male was not in evidence in any of his accustomed places. After systematic search I found him many yards from the ledge among low ragweeds on the adjacent level area. Attempting to drive him toward the ledge, I moved slowly toward him. He made several short dashes toward the ledge, but he became increasingly reluctant to go farther in that direction. After each dash he would crouch on the bare ground seeking to escape attention. Moving slowly I was able to approach and almost touch him with my extended finger. He wriggled his tail tip, and opened his mouth in a threatening defensive gesture before moving on. When he had been driven to within ten feet of the ledge, the larger male perched there made bobbing display movements and ran forward. The small male saw his adversary, and could not be driven farther toward the ledge. After unsuccessful efforts to drive him in that direction, I noosed him and tethered him at one of his usual basking places. The other male was watching intently from a vantage point twenty feet away. As I stepped back, this male rushed to the attack, pausing at a distance of six feet to turn sideways for a spectacular brief display. Then he closed in on the tethered male and they instantly caught each other in their jaws, wrenching violently as they rolled and writhed about. The larger male seemed to be watching me even at the height of the struggle. My attempt to obtain a photograph at a distance of three feet caused the larger male to run six feet. Then he squared around and displayed vigorously. Before the fight, during it and afterward, there was striking difference in color between the two males. The larger was bright green while the smaller was dull green suffused with gray and brown.

Neither male evidenced any serious injury from the fight. However, the smaller male promptly hid when he was released, and was never seen again. It is unlikely that he was killed outright in combat, but probably his elimination was an indirect result of his displacement by the larger male.

Before the smaller adult male was eliminated in August, 1950, a younger male hatched in August, 1949, was already approaching adult size, and his chosen area was within the stretch of ledge occupied by the smaller adult. This young male was dominated by both the adult males. Probably because they had been familiar with him since he was a small juvenile, and had not been challenged by him, both adults were surprisingly tolerant of him. They would permit him to bask on the ledge only a few yards away. After the disappearance of the smaller adult, this young male took over the west part of the ledge formerly occupied by the adult, and this part was only occasionally invaded by the surviving adult male. In 1952 this older male had been eliminated, and the younger, freed from opposition and grown to fully adult size, then ranged more widely, encroaching into the former territory of the older. He was last recorded on June 2, 1952. A month after his disappearance the single surviving young male of the 1951 brood was approaching adult size. By August this newly matured male ranged over the entire length of the quarry ledge unopposed, as the only other individuals present were two old females and five hatchlings. In 1953 this male evidently moved away from the main ledge and settled at some nearby outcrop as he was seen only twice—in early April just after emergence, and again in mid-July. In his absence in the spring of 1953 the ledge was left to four young males of the 1952 brood, with two young females and two old females. Each of the young males established a territory, and fights were frequent. By early May one was eliminated and in early June another was missing. By then the remaining two were approaching adult size; they had divided the quarry ledge into two territories and each kept to his own half. One disappeared in May, and soon afterward the other extended his territory to include the vacated area. Four young males of the 1953 brood survived to the spring of 1954, but in a few weeks, by early June, all had been eliminated, as the one adult male ranged widely over the entire quarry area.

On May 28, 1953, an adult male captured in Anderson County, Kansas, was brought to the quarry and experimentally tethered beside one of the usual territorial perches of a young male. The young male at that time had a snout-vent length of 82 mm. (contrasted with 100 mm. in the adult) and a weight of 18 grams (a little less than half the adult weight). Despite this severe handicap, the young male rushed without hesitation, to the defense of his territory. Two feet from the intruder he paused momentarily, turning sideways and making vigorous bobbing display movements, with his gular pouch expanded. Then he rushed at the larger lizard and drove him off the ledge. The tethered adult male lunged about in a frantic effort to escape, but even while I was attempting to disentangle him from a weed clump, the smaller one ran down and menaced him, seeming almost indifferent to my presence. The larger lizard threatened his attacker with gaping jaws and he fought back when attacked but only to defend himself. His colors remained dull and he did not display. He was so much larger and more powerful that it seemed that he could have killed or maimed his diminutive adversary with a single well placed bite. To avoid injury to the smaller male I removed the larger after reactions of both had been tested. The bold aggressiveness on the part of the smaller male, and the timidity and lack of spirit on the part of the larger were equally impressive, both illustrating the important role of territory in the male combat of this species. As in other kinds of animals that are strongly territorial, the individual on his home area is at a psychological advantage, and fights his best, while one that is transferred to strange surroundings makes a poor showing even against a smaller and weaker opponent.

Greenberg (1945: 227) in his study of the social behavior, observed no hostility on the part of females. However, the females in the colony at the quarry were never closely associated, tending to be well spaced. On a few occasions hostile behavior was noted among them. On June 9, 1951, an adult female which had recently acquired postnuptial red marks, was seen to display and then chase a second adult female, the latter lacking red marks. Both had been noted closely associated with the same male at different times within a few days. The female that was the aggressor in the foregoing observation, again had red postnuptial marks on May 30, 1952, and on that date was experimentally tested by releasing near her and her mate another adult female from the opposite end of the ledge. The resident female moved up to the newcomer with mildly aggressive behavior, flattening her body dorsoventrally and darting out her tongue. She did not attack, but soon moved away, followed by the male. On May 15, 1954, the female of a courting pair suddenly left her mate and rushed at an immature female which had appeared on the ledge about five feet away. The larger female chased the other approximately 15 feet, staying close behind it and biting it twice while the pursuit was in progress. When the one pursued escaped and hid, the other returned to the male.

Males and females are often associated in pairs even at times when there is no breeding activity. Individuals of the opposite sex, so far as observed, were never objects of territorial hostility. Females that are sexually immature flee from males that attempt to court them, but at other times may tolerate their presence or even seek it. On several occasions young females alarmed by the presence of a person, and fleeing along the ledge, came to a stop perching on the back of an adult male. Neither adult males nor adult females have been seen to show hostility toward small young, nor to take any notice of them whatsoever. However, the young are wary of larger individuals, and the adults may catch and eat them occasionally (Burt, 1928a: 51).

Hatchlings at first are timid and tend to avoid others, and are not attached to definite areas. When they have become familiar with their surroundings, and have chosen look-outs and basking places, they are still tolerant and two or more may be found within a few feet of each other. Intolerance is first noticeable when the young are several weeks old and have approximately doubled their length at hatching. On September 30, 1953, the young males, then approximately seven weeks old and 75 to 80 mm. in snout-vent length, were found to be almost uniformly spaced along the ledge. One that was caught was released 30 feet farther along the ledge, near where a smaller one was basking. The latter displayed. The one released crouched, flattening against the rock. When he was prodded with a stick and caused to move a few inches, the other rushed at him, and they darted eight feet along the steep bank. The intruder found concealment crouching under a clump of grass, and the pursuer perched alertly on a rock a foot away. On this date the young males' red spots had become dull and faint in some and had completely disappeared in others. The bright spots of the juvenal males probably are social releasers of some kind. They may serve to inhibit attack, especially by larger males.

FOOD HABITS

The collared lizard hunts by sight. Ordinarily the prey must be in motion to attract the lizard's attention. The usual technique in hunting is to watch from the top of a rock a few inches above the level of the surroundings. Any small animal flying or walking within a radius of several yards immediately attracts the lizard's attention, and is taken with a sudden rush, crushed in the jaws, and gulped down entire. Hurter (1911: 130) noted that the collared lizard can catch flying insects, jumping as much as 18 inches to bring them down.

Although the food consists predominantly of arthropods, various observers have reported predation on smaller lizards: in southern California, *Cnemidophorus tigris* (Cowles, 1920: 64) and *Uta stansburiana* (Johnson, Bryant and Miller, 1948: 259); in Arizona, *Sceloporus* sp. (Klauber, 1939: 85), and small rock-inhabiting lizards (presumably *Uta stansburiana,* Springer, 1928: 100); in New Mexico, *Phrynosoma modestum* (Little and Elbert, 1937: 219); and in Kansas, the young of its own species (Burt, 1928a: 51). In captivity the collared lizard has also been noted to feed upon *Cnemidophorus sexlineatus* (Hurter, *loc. cit.*) and *Eumeces obsoletus* (Burt, 1933: 188). Woodbury (1928: 15) reported that in Zion National Park, Utah, collared lizards were sometimes seen chasing smaller lizards, *Cnemidophorus* and *Sceloporus.*

Blair and Blair (1941: 230-232) examined stomachs of 91 from northeastern Oklahoma and found 314 food items: 214 orthopterans (mostly grasshoppers), 29 coleopterans, 16 lepidopterans, 8 hemipterans, 8 hymenopterans, 6 dipterans, 3 neuropterans, 2 homopterans, 18 arachnids, 2 snails and 1 centipede. The Orthoptera included 19 genera and 30 species and they constituted the entire contents of several samples. The lepidopterans, coleopterans, and arachnids were represented mainly in the late March sample, before grasshoppers were abundantly available. Knowlton (1938: 236) and

Knowlton and Thomas (1936: 64) studied stomach contents of 107 from western Utah. Of the 584 items identified there were 213 orthopterans (mostly grasshoppers), 168 hymenopterans (only 19 of which were ants), 87 coleopterans, 51 lepidopterans, 22 dipterans, 19 homopterans, 11 hemipterans, 9 spiders, 2 neuropterans, and 1 odonatan. Stomach contents of the 16 specimens from Kansas (Burt, *loc. cit.*) consisted of Orthoptera 88.3%, Lepidoptera 6.6%, Arachnida 4.1%, and Coleoptera 1%.

Other published statements concerning the food habits are based on few records. Ruthven (1907: 513) found that a kind of large grasshopper was the chief item in stomachs of 11 from southern New Mexico and Arizona; other locustids, and beetles also had been eaten. Springer (*loc. cit.*) in Arizona and Johnson, Bryant and Miller (*loc. cit.*) in California, each found that grasshoppers were the chief food. Camp (1916: 52) found grasshoppers, other orthopterans, and small beetles in stomachs of two from southeastern California. Little and Elbert (1937: 219) recorded a grasshopper, cicadas, and fragments of other insects in stomachs of four from southwestern New Mexico. Ruthven and Gaige (1915: 17) found insects, spiders, and vegetation (perhaps taken accidentally) in stomachs of two from northeastern Nevada. Force (1925: 26) found locustids, carabids, formicids, myrmicids and arachnids in stomachs of nine from Oklahoma. Hallowell (1856: 239) found grasshoppers and beetles in one from Texas.

In 1951 I examined stomachs of five collected in Wabaunsee County, Kansas, on May 13, and 13 collected in Anderson County on June 17. One of these 18 stomachs was empty. The other 17 contained a total of 33 prey items: 9 grasshoppers, 8 beetles (including 2 scarabaeids, a buprestid and several that were probably carabids), 6 spiders (5 of the genus *Phidippus* and the remaining one also a salticid), 5 vespid wasps, 2 halictid bees and one each of grouse locust, lepidopteran larva, and unidentified insect.

The collared lizards caught and examined at the quarry nearly always had their faces or chins stained with the dark brown buccal secretions of grasshoppers. On several occasions I tested the feeding reactions of tamer individuals by tossing grasshoppers onto the rocks near them. With a sudden rush the lizard would snap up the grasshopper almost as soon as it touched the rock.

In catching other arthropods the lizards were at times more circumspect. On one occasion a robust, two-inch, red centipede was seen to dart across an open rock surface three feet from a young male. The latter rushed in pursuit, caught it by the head, bit it and shook it and then threw it down. The attack was repeated several times, but each time after dropping the centipede, the lizard shook its head as if it had been bitten. Severely injured, the centipede ran backwards slowly in a circular course. The lizard paused beside it for a few seconds and gave the head end a final bite, then dropped it and ran back to his rock perch a few feet away. An adult wheel bug (*Arilus cristatus*) was released near an adult male. When the bug moved, the lizard ran to it and seized it, but instantly released it and retired. The bite of this large reduviid is painful to humans but seemingly the lizard had been repulsed by its noxious secretion rather than bitten. On several occasions large predaceous ground beetles (*Pasimachus*) that were abundant along the ledge, were thrown down near basking collared lizards. The lizards always showed some interest in the fleeing beetles, even to the point of pursuing them, but did not actually attack, perhaps deterred by memory of the caustic defensive secretion with which these beetles defend themselves.

To determine the food sources of the collared lizards at the quarry I collected and studied scats. These are of characteristic appearance, usually one inch to two inches in length, and one-fourth inch or a little more in diameter. They accumulate on or about the lizards' look-outs. By their presence and distribution a collector often may be guided to the rock on which the lizard habitually basks, and beneath which it may have sought shelter. A total of 325 scats were examined, and 456 prey items were recorded: orthopterans, 46.6%; beetles, 16.5%; spiders, 15.5%; unidentified insects, 11.9%; hymenopterans, 3.3%; cicadas, 3.1%; five-lined skinks, 2.0%; phalangids, .9%; hemipteran, .2%. The condition of the remains was variable, and for some groups of prey animals no adequate reference material was at hand. In many instances items could not be allocated to family or even to order. Specific determinations were made for a little more than one-third of the total items.

In studies of food habits, scatological material is unsuitable for determining the volumetric ratios of different kinds of prey. However, in the collared lizard, which feeds upon prey within a fairly narrow size range, and gulps down each prey item entire, the relative frequencies of occurrence of different items may approximate their relative bulk in the diet. Usually each recorded occurrence of prey represented one individual animal—the chelicerae and fragments of legs of spiders; the heads, pronota, wings and leg fragments of grasshoppers; the broken elytra and legs of beetles;

and the scales, with only an occasional bone, of the skinks. Grasshoppers, cicadas and skinks, the more bulky items eaten, obviously made up greater parts of the diet than indicated by their percentages of frequency of occurrence. Most of the spiders, harvestmen and wasps were relatively small items, and their frequency of occurrence was greater than their actual importance in the diet.

The 213 orthopterans included 4 unspecified, 9 grouse locusts, 4 gryllid crickets, 2 ceuthophilid crickets, and 194 grasshoppers. The latter included 79 unspecified (because remains were meager or extremely fragmentary and discolored), 54 *Melanoplus bivittatus*, 25 *Arphia simplex*, 21 *Melanoplus femur-rubrum*, 9 *Melanoplus* sp., 5 *Dissosteira carolina*, and 1 *Melanoplus differentialis*. The 75 beetles included many more kinds, and no specific determinations were made. Tentative family allocations include: 15 scarabaeids, 14 curculionids, 8 meloids, 2 carabids, 2 buprestids, 1 elaterid, and 1 chrysomelid. Nearly all the beetles were within the size range one inch to one-half inch. Of the 71 spiders, 38 were the large black jumping spider, *Phidippus audax* and 17 identifiable only as *Phidippus* probably belonged to this same species, in most instances at least. This spider was abundant among the rocks where the lizards lived. Many of the jumping spiders found in the scats were immature. Twelve were wolf spiders, probably all of the genus *Lycosa*. One was a common grass living species, *L. rabida*, and several others were tentatively identified as *L. aspersa*. The 14 cicadas were probably all of the same species, a large *Tibicen*. The 15 hymenopterans included vespid wasps, and one carpenter ant (*Camponotus herculaneus*). The nine five-lined skinks were mostly hatchlings. Their remains consisted largely of scales.

Scats were collected at the quarry each year of the study, 8 in 1949; 54 in 1950; 126 in 1951; 41 in 1952; 104 in 1953; and 7 in 1954. The ratios of the different prey items in successive samples fluctuated, doubtless influenced by many factors, including stage of the season, the course of plant succession on the area, the weather, and the preferences of individual lizards. The relative importance of these factors was not evident in most instances. The 1950 sample included 8 of the 9 grouse locusts and 7 of the 12 lycosid spiders. Otherwise 1951 afforded the greatest contrast. In that year precipitation was far above normal and temperature averaged abnormally low. Weather conditions were especially unfavorable for grasshoppers which were relatively scarce. Many were found dead or dying from fungus infections or other disease. The collared lizard colony was unfavorably affected by the cool, wet weather and perhaps also, by the effect of this weather in reducing the main food source. One of the three adult females failed to breed, and the other two bred late, with poor success. The relative scarcity of grasshoppers was compensated for by increased predation on other kinds of large insects. For several of the more important food species the 1951 sample is contrasted with the combined samples from other years in Table 9.

TABLE 9.—PERCENTAGES OF VARIOUS ITEMS IN 1951 SAMPLE AND IN COMBINED SAMPLES FROM OTHER YEARS.

	1951	Other years
Total items	179	277
Grasshopper	24.6%	55.6%
Beetle	31.2%	9.4%
Phidippus	14.5%	11.2%
Other spider	2.8%	2.5%
Wasp	5.6%	1.1%
Skink	3.3%	1.1%
Cicada	6.7%	1.4%

PREDATION

Snakes and raptorial birds are among the chief enemies of collared lizards. In most instances the fates of those that disappeared from the quarry were not definitely known. However, the broad-winged hawk (*Buteo platypterus*) seemed to be by far the most important natural enemy on this area. Each year of my field study a pair of these hawks had a territory which included the quarry and on many occasions the arrival of a person caused one of these hawks to flush from a favorite perch, an old post near the center, which overlooked the entire area. The availability of collared lizards may have been the attraction, although other known prey, including young cottontails, voles, skinks, small snakes, and nestling birds, also might have been secured there. No actual captures of the lizards by the hawks were witnessed. However, in the summer of 1954, the hawks' nest was found and on two occasions collared lizards were recorded in the prey remains palped from the gullet of a young hawk. One of the two lizards eaten was a female nearly five years old. This old female was especially shy and elusive, ordinarily venturing only a few inches from the crevice where she usually sought shelter. When the hawk caught her, she was ready to lay, and she may have been taken by surprise while in search of a nest site or excavating a burrow for her eggs.

The red-tailed hawk (*Buteo jamaicensis*), marsh hawk (*Circus cyaneus*), and Cooper's hawk (*Accipiter cooperi*) also present on the area, were possible predators on the colony at the quarry. All of them occur throughout the collared lizard's range and probably prey on it to some extent. The sparrow hawk (*Falco sparverius*), prairie falcon (*Falco mexicanus*), and Swainson's hawk (*Buteo swainsoni*) also probably prey upon the collared lizard, but I know of no specific records.

Burt (1928a: 62) recorded that a Great Plains skink (*Eumeces obsoletus*) killed and ate a small collared lizard in captivity. Brooking (1934: 96) recorded that a striped racer (*Masticophis taeniatus*) collected by him in Malheur County, Oregon, contained a collared lizard, swallowed tail first. Mr. Richard B. Loomis discovered a blue-racer (*Coluber constrictor*) attacking an adult collared lizard near Garnett, Anderson County, Kansas, on May 4, 1952. The thrashing movements of the snake's body attracted the observer's attention to it. The racer's head was beneath a rock, and it had secured a hold on the lizard's head. When collared lizards are inactive, in shelter under rocks or in burrows, they may be caught by snakes, including the more slowly moving kinds as well as the racers. The blue-racer, striped racer, whip snake (*Masticophis flagelliformis*) and other racers probably are among the more important enemies, as they hunt by sight in open situations and are swift enough to catch the lizards on the run.

Klauber (1939: 85) wrote that *C. c. baileyi* takes refuge under stones and is usually easy to capture by a quick grab when the stone is overturned. In many of the localities where I have found collared lizards, the boulders beneath which they sought shelter were small enough to be turned. Often I have hunted them by turning boulders and trying to catch the lizard beneath with a sudden grab. If, as seems probable, hawks and snakes are the chief natural enemies, the lizards may seldom need to cope with such emergencies. Those exposed by lifting rocks were always confused and were inefficient in escaping despite their great speed in running. One suddenly exposed in its hiding place might dash away for a few yards and then return time after time to the site of its former shelter, running in an erratic and utterly confused manner over the ground where the rock had lain. Young only a week or two old have been noted to behave similarly, and obviously had already become familiar with their surroundings and had learned to depend on one strategically located shelter for escape.

Often the hiding place sought is a hole or crevice beneath the boulder on which the lizard is perched, but sometimes the lizard runs to one that is several or many yards away. Individuals and populations differ greatly in their degree of wildness, and in both innate and learned reactions to persons or other potential enemies. Those of the colony at the quarry were most noticeably different. They would readily permit a person to approach to within a few yards, and would not take shelter when hard pressed, but would merely move away a short distance without showing more than mild alarm. These lizards became skilled in avoiding proximity or contact of the noose stick and the wire attached to it.

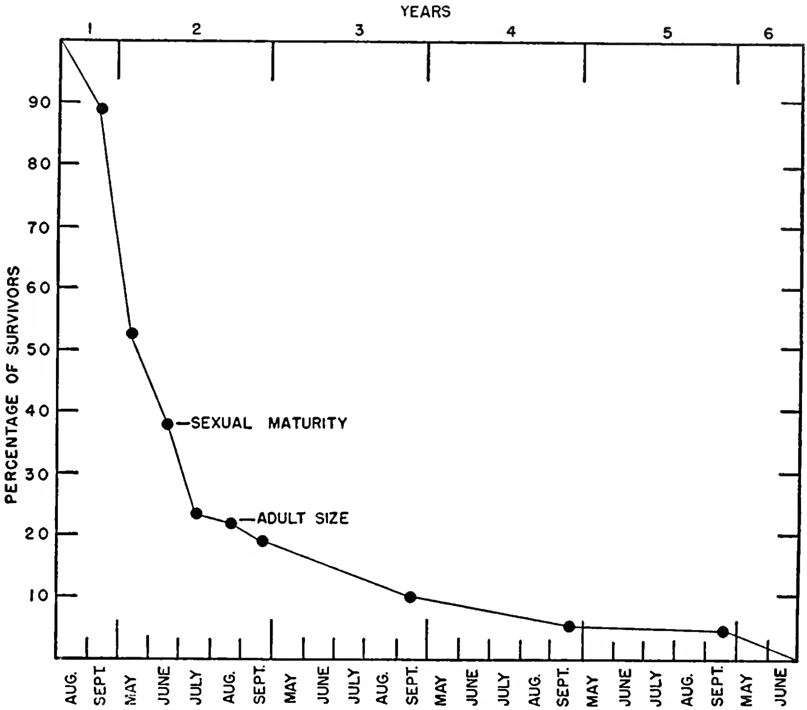


Fig. 10. Graph of survivorship in the population of collared lizards studied. Mortality is high in the first few months, but after adult size is attained, the lizards live in relative security.

Young that are less than a week old differ from adults in their escape reactions. Being still unfamiliar with their surroundings, they do not retreat directly to appropriate escape shelters, but run about erratically, darting into any hiding place that can be found. The places of concealment chosen are often entirely inadequate, leaving part of the lizard exposed to view.

Burt (1933: 188) recorded an instance of a young collared lizard jumping into the web of a large spider, from which it was unable to free itself. I observed a similar incident at the quarry. The web was that of a funnel weaver (*Agelena naevia*).

Burt and Hoyle recorded that a large adult male alarmed by movements of a person, ran downhill and dived into a pool of muddy water to escape. Similar incidents have been observed for many other kinds of lizards, and it seems likely that in most instances the fleeing lizards entered the water unintentionally. Ruthven (1907: 513) wrote that in southern Arizona these lizards when alarmed would run swiftly from bush to bush, often for several rods.

Woodbury (1907: 513) contrasted the escape reactions of an individual basking to warm itself in the sunshine, which ran only a short distance and crouched motionless depending on concealment, with the behavior of the same individual alarmed while it was fully warmed and foraging. In the latter instance it escaped by running. At the quarry this difference in behavior according to temperature was conspicuous. At times when the air was cool and the sun was low, those lizards that were in the open were especially loath to leave their basking places. Under such conditions I found that the most effective way of catching them was to approach very slowly until my hand was within a few inches, and then secure the lizard with a sudden grab. Dozens of captures were made in this manner. The lizards were usually only a few degrees below optimum body temperature, or in some instances, at approximately the optimum. Once flushed, their movements were exceedingly rapid.

Many observers have noted bipedal running in the collared lizard, and in various other iguanids and agamids. The quadrupedal gait is usual when the lizard is walking, or running unhurriedly, or for short dashes. However, as the lizard gains speed, the forebody is elevated to approximately a 45° angle with the substrate and the forefeet are held clear of the ground. Ordinarily the movements of a lizard running at full speed are so rapid that they are blurred to human vision. Bipedal running is best observed in those that are well below the optimum temperature level and are relatively slow. Snyder (1952) studied bipedal locomotion in the collared lizard and other lizards by motion picture analysis, with a camera speed of between 1000 and 1500 frames per second. He found that a collared lizard running at full speed has a stride approximately three times the snout-vent length, which would be roughly one foot in a full grown lizard.

PARASITES

Klauber (1939: 83) noted that collared lizards in California and Arizona frequently were infested with orange or vermilion colored mites. Chiggers were common on the collared lizards of the colony at the quarry on the Reservation. Many of these chiggers were collected and identified, and all were found to be *Trombicula alfreddugèsi,* the common pest chigger, although various other genera and species have been recorded from other vertebrate hosts on the Reservation (Loomis, 1955). Chiggers usually appeared on the lizards near the end of May or in the first or second week of June each year. In June, Loomis found an average of more than 200 chiggers on adult collared lizards. The young lizards generally had fewer chiggers in proportion to their smaller body surface areas. Later in the summer infestations became progressively lighter. Infestations are most severe in hot, humid weather. The chiggers tend to concentrate in protected places, in the axilla, the groin, the edges of the gular fold, and the eyelids. In the folds of skin at these sites the chigger is partly protected from direct sunlight and dry air. The collared lizard's habit of basking in sunlight probably protects it from chiggers to some extent. Also, its frequent molts rid it of many chiggers. Dried and dead chiggers often may be found still attached to patches of sloughed skin. Lizards that had recently molted were relatively free of chiggers.

Loomis found that collared lizards from Anderson County, Kansas, were infested with *Trombicula lipovskyana* as well as with *T. alfreddugèsi.* Collared lizards from south-central Kansas had both *T. alfreddugèsi* and *Acomatacarus arizonensis.* Chiggers were the only ectoparasites found on the lizards. Nothing was learned concerning the internal parasites.

SUMMARY

A colony of collared lizards, 61 in all, were observed in six different seasons, 1949 through 1954, along the limestone ledge of a deserted quarry in the northeastern corner of Douglas County, Kansas. The numbers present at any one time varied from a maximum of 23 to a minimum of one. Usually there were two to six adults and a larger number of young.

The information obtained from this small colony was supplemented by the writer's observations on these lizards at other localities in Kansas, and in more remote parts of the range, and by the published writings of numerous authors who have observed details concerning the habitat, behavior, reproduction, food, or natural enemies.

These lizards are nearly always limited to open, rocky situations and require boulders to perch upon as look-outs. In the northeastern part of its range the species is represented by scattered colonies which seem to be relicts from a time when the region offered more favorable habitat—perhaps as little as 100 years ago, before prairie fires holding back the woodlands were brought under control, but more probably at a much earlier time when climate was warmer and drier. Throughout its range the collared lizard populations are scattered and isolated more or less because of the restricted nature of the habitat.

In northeastern Kansas these lizards emerge from hibernation in April or early May after several days of warm weather. In hibernation they endure temperatures near freezing or possibly a little below. At 6° C. or below, one cannot be fully roused from torpor. At 11.8° C. it is barely able to walk. Individuals have been found in the open at air temperatures as low as 13.5° C. Over a wide range of air temperatures the lizards, through thermoregulatory behavior, maintain relatively high body temperatures usually between 37° and 40°. They are active chiefly at air temperatures well below this level, and depend on insolation for warmth. On cloudy days activity is much reduced even though the temperature remains high. The lizards usually seek shelter when they are unable to maintain body temperatures higher than 30° C., but body temperatures as low as 20.7° have been recorded. The highest temperature recorded as voluntarily tolerated was 43.3°. One heated to 45° showed discomfort but was unharmed.

Breeding occurs chiefly in late May and early June, and may include young hatched the preceding August, as growth is remarkably rapid and sexual maturity is attained when the lizard is still short of adult size.

In courtship the male displays to the female and slithers over and around her nipping her from time to time. The receptive female may actively seek a male. She responds to his courtship with a stereotyped posturing, and accepts copulation. Pairs may be found in close association at any time during the active season. In basking they lie side by side or in actual contact. Females that have been impregnated develop bright scarlet marks along the sides of the body within three or four days, with accompanying physiological changes causing them to resist vigorously the male's attempts at courtship, though remaining tolerant of him otherwise. Evidently laying occurs 16-19 days after insemination and the "postnuptial" scarlet marks of the female are retained for several weeks after laying. Under favorable conditions the female may produce a second clutch of eggs two or three weeks after the first one. According to the literature, clutch size varies from 2 to 24 eggs. The average of 29 clutches is 7.55 ± .70. Approximate incubation periods under natural conditions varied from 52 to 94 days, evidently depending on temperature, which was affected both by weather and by site of the nest.

Collared lizards molt frequently. The skin is sloughed off in several large patches with but little loss of moisture. Molt is most frequent in the rapidly growing young. In those that hatch in early August and remain active until late September, four molts seem to be most typical for the 7-8 weeks prehibernation period. In the next growing season the young attain adult size and there are typically five molts. The average interval of molt was 23 days. In adults also, five molts per season is most typical, and intervals between molts average 25.4 days.

Growth is most rapid in the first week of life, when the daily increase in snout-vent length may exceed 1 mm. At an age of 8 weeks the young may have doubled their original length of approximately 40 mm., and are gaining in length at only about one-fifth of the rate of hatchlings. At the outset, the growth rate is similar in males and females, but in half-grown young the rate in females is only about eighty per cent of that in males. The males grow to an average length and bulk greater than those of females. A lizard may attain average adult size at an age of a year but it continues to make slight gains in its second, third and fourth years.

Young are eliminated rapidly through natural causes, and nearly half fail to survive to the time of hibernation. Evidently there is some loss during hibernation but it cannot be measured accurately. After hibernation, in larger young the incidence of mortality is high also. Evidently many are eliminated as a result of territorial pressure forcing them out of the more favorable habitat.

Like many other iguanids, these lizards have territoriality well developed, and each tends to stay within its chosen area, defending it against others. Territoriality is strongly developed in the adult male, and he excludes other adult males from the area that he occupies, sometimes by pursuit and combat, more often by stereotyped displays, in which his bright colors are shown off to greatest advantage. The male is, however, tolerant of young, even of smaller males that have become sexually mature, if they do not challenge his dominance. The male's territory may overlap those of one or more females. A male may associate with two or more females at different times in the same day. Females usually stay within areas much smaller than those occupied by males. Territoriality is less strongly developed in females which, however, tend to occupy mutually exclusive areas. Adult females occasionally show hostile behavior toward other adult females or those that are subadult.

Young males that are less than half-grown in bulk and less than 80 per cent of full length may mature sexually and may defend territories, even against intruding males that are fully adult. Young males, however, recognize the dominance of an adult male already resident and do not challenge him.

These lizards are diurnal and hunt by sight. The usual method of hunting is to watch from an elevated look-out and secure moving prey with a sudden rush. Large insects make up most of the food. Nearly all published accounts of the food habits indicate that grasshoppers are the most important food. On the Reservation, grasshoppers made up 46.6 per cent of the items recorded. Other kinds of prey regularly fed upon were, in order of their importance, beetles, spiders, wasps, cicadas, and skinks. There are published records of collared lizards eating smaller lizards including the whiptail, scaly lizard, brown-shouldered lizard, horned toad, Great Plains skink, and even hatchlings of their own species. On the study area, the five-lined skink, which was the only common small lizard, made up two per cent of the recorded food items.

Known natural enemies include the broad-winged hawk, striped whip snake, and blue-racer. Hawks and snakes of these and other species probably are the chief predators. In time of danger the lizard may hide at the base of a thick clump of bushes, but more often it seeks shelter in a rock-crevice or burrow. One that is caught or cornered fights fiercely, and the powerful jaws are capable of inflicting a painful bite.

The ectoparasites include several kinds of chiggers. Because of the lizard's habit of basking in hot and dry places, these chiggers are closely confined to the more protected areas of the body surface, notably the axilla, where they often occur in small clusters.

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(Continued from inside of front cover)

19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-317. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

***Vol. 6.** (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.

2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
6. Distribution of Some Nebraskan Mammals. By J. Knox Jones. Pp. 479-487. April 21, 1954.
7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
8. A new subspecies of bat (Myotis velifer) from Southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.
9. Mammals of the San Gabriel Mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.
10. A new bat (Genus Pipistrellus) from Northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.
11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.
12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.
13. A new cottontail (Sylvilagus floridanus) from Northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.

(Continued on back of cover)

(Continued from inside of back cover)

14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.
15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

Vol. 8.
1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, Pls. 1-2, 26 figures in text. September 1, 1954.
2. Myology and serology of the avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.
3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, pls. 3-6, 10 figures in text, 9 tables. February 10, 1956.

More numbers will appear in volume 8.

Vol. 9.
1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extensions of known ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

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A FIELD STUDY
OF THE KANSAS ANT-EATING FROG, GASTROPHRYNE OLIVACEA

By

Henry S. Fitch

INTRODUCTION

The ant-eating frog is one of the smallest species of vertebrates on the University of Kansas Natural History Reservation, but individually it is one of the most numerous. The species is important in the over-all ecology; its biomass often exceeds that of larger species of vertebrates. Because of secretive and subterranean habits, however, its abundance and effects on community associates are largely obscured.

The Reservation, where my field study was made, is the most northeastern section in Douglas County, Kansas, and is approximately 5½ miles north and 2½ miles east of the University campus at Lawrence. The locality represents one of the northernmost occurrences of the species, genus, and family. The family Microhylidae is a large one, and most of its representatives are specialized for a subterranean existence and a diet of termites or ants. The many subfamilies of microhylids all have distributions centering in the regions bordering the Indian Ocean, from South Africa and Madagascar to the East Indies, New Guinea, and Australia (Parker, 1934). Only one subfamily, the Microhylinae, is represented in the New World, where it has some 17 genera (de Carvalho, 1954) nearly all of which are tropical. G. *olivacea,* extending north into extreme southern Nebraska (Loomis, 1945: 211), ranges farther north than any other American species. In the Old World only *Kaloula borealis* has a comparable northward distribution. Occurring in the vicinity of Peiping (Pope, 1931: 587), it reaches approximately the same latitude as does *Gastrophryne* in Nebraska. The great majority of microhylid genera and species are confined to the tropics.

Nearly all ant-eating frogs seen on the Reservation have been caught and examined and individually marked. By November 1, 1954, 1215 individuals had been recorded with a total of 1472 captures. In the summer of 1950, Richard Freiburg studied this frog on the Reservation and his findings (1951) led to a better understanding of its natural history. The numbers of frogs studied by him however, were relatively small and the field work was limited to the one summer. The data now at hand, representing six consecutive years, 1949 through 1954, serve to supplement those obtained by Freiburg, corroborating and extending his conclusions in most instances, and also indicating that certain of his tentative conclusions need to be revised.

While the present report was in preparation, Anderson (1954) published an excellent account of the ecology of the eastern species *G. carolinensis* in southern Louisiana. Anderson's findings concerning this closely related species in a much different environment have been especially valuable as a basis for comparison. The two species are basically similar in their habits and ecology but many minor differences are indicated. Some of these differences result from the differing environments where Anderson's study and my own were made and others certainly result from innate genetic differences between the species.

The frog with which this report is concerned is the *Microhyla carolinensis olivacea* of the check list (Schmidt, 1953: 77) and recent authors. De Carvalho (1954: 12) resurrected the generic name, *Gastrophryne,* for the American species formerly included in *Microhyla,* and presented seemingly valid morphological evidence for this plausible generic separation.

G. olivacea is obviously closely related to *G. carolinensis;* the differences are not greater than those to be expected between well marked subspecies. Nevertheless, in eastern Oklahoma and eastern Texas, where the ranges meet, the two kinds have been found to maintain their distinctness, differing in coloration, behavior, calls, and time of breeding. Hecht and Matalas (1946: 2) found seeming intergrades from the area of overlapping in eastern Texas, but some specimens from this same area were typical of each form. Their study was limited to preserved material, in which some characters probably were obscured. More field work throughout the zone of contact is needed. The evidence of intergradation obtained so far seems to be somewhat equivocal.

Besides *G. olivacea* and typical *G. carolinensis* there are several named forms in the genus, including some of doubtful status. The name *mazatlanensis* has been applied to a southwestern population, which seems to be a well marked subspecies of *olivacea,* but as yet *mazatlanensis* has been collected at few localities and the evidence of intergradation is meager. The names *areolata* and *texensis* have been applied to populations in Texas. Hecht and Matalas (1946:

3) consider *areolata* to be a synonym of *olivacea,* applied to a population showing intergradation with *carolinensis,* but Wright and Wright (1949: 568) consider *areolata* to be a distinct subspecies. *G. texensis* generally has been considered to be a synonym of *olivacea.* Other species of the genus include the tropical *G. usta, G. elegans* and *G. pictiventris.*

Of the vernacular names hitherto applied to *G. olivacea* none seems appropriate; I propose to call the species the Kansas ant-eating frog because of its range extending over most of the state, and because of its specialized food habits. The type locality, originally stated to be "Kansas and Nebraska" (Hallowell, 1856: 252) has been restricted to Fort Riley, Kansas (Smith and Taylor, 1950: 358). Members of the genus have most often been referred to as toads rather than frogs because of their more toadlike appearance and habits. However, this family belongs to the firmisternial or froglike division of the Salientia and the terms "frog" and "toad," originally applied to *Rana* and *Bufo* respectively, have been extended to include assemblages of related genera or families. Members of the genus and family usually have been called "narrow-mouthed" toads from the old generic name *Engystoma,* a synonym of *Gastrophryne. G. olivacea* usually has been referred to as the Texas narrow-mouthed toad, or western narrow-mouthed toad. The latter name is inappropriate because the geographic range is between that of a more western representative (*mazatlanensis*) and a more eastern one (*carolinensis*). The names *texensis, areolata* and *carolinensis* have all been applied to populations in Texas, and it is questionable whether typical *olivacea* even extends into Texas.

HABITAT

In the northeastern part of Kansas at least, rocky slopes in open woods seem to provide optimum habitat conditions. This type of habitat has been described by several earlier workers in this same area, Dice (1923: 46), Smith (1934: 503) and Freiburg (1951: 375). Smith (1950: 113) stated that in Kansas this frog is found in wooded areas, and that rocks are the usual cover, but he mentioned that outside of Kansas it is often found in mesquite flats that are devoid of rocks. Freiburg's field work was done almost entirely on the Reservation and was concentrated in "Skink Woods" and vicinity, where much of my own field work, both before and afterward, was concentrated. On the Reservation and in near-by counties of Kansas, the habitat preferences of the ant-eating frog and the five-lined skink largely coincide. In an account of the five-lined skink on the Reservation, I have described several study areas in some detail (Fitch, 1954: 37-41). It was on these same study areas (Quarry, Skink Woods, Rat Woods) that most of the frogs were obtained.

Although *G. olivacea* thrives in an open-woodland habitat in this part of its range, it seems to be essentially a grassland species, and it occurs throughout approximately the southern half of the Great Plains region. Bragg (1943: 76) emphasized that in Oklahoma it is widely distributed over the state, occupying a variety of habitats, with little ecological restriction. Bragg noted, however, that the species is rarely, if ever, found on extensive river flood plains. On various occasions I have heard *Gastrophryne* choruses in a slough two miles south of the Reservation. This slough is in the Kaw River flood plain and is two miles from the bluffs where the habitat of rocky wooded slopes begins that has been considered typical of the species in northeastern Kansas. It seems that the frogs using this slough are not drawn from the populations living on the bluffs as Mud Creek, a Kaw River tributary, intervenes. The creek channel at times of heavy rainfall, carries a torrent of swirling water which might present a barrier to migrating frogs as they are not strong swimmers. The frogs could easily find suitable breeding places much nearer to the bluffs. Those using the slough are almost certainly permanent inhabitants of the river flood plain. The area in the neighborhood of the slough, where the frogs probably live, include fields of alfalfa and other cultivated crops, weedy fallow fields, and the marshy margins of the slough. In these situations burrows of rodents, notably those of the pocket gopher (*Geomys bursarius*), would provide subterranean shelter for the frogs, which are not efficient diggers.

The frogs may live in many situations such as this where they have been overlooked. In the absence of flat rocks providing hiding places at the soil surface, the frogs would rarely be found by a collector. The volume and carrying quality of the voice are much less than in other common anurans. Large breeding choruses might be overlooked unless the observer happened to come within a few yards of them. Most of the recorded habitats and localities of occurrence may be those where the frog happens to be most in evidence to human observers, rather than those that are limiting to it or even typical of it.

On September 20, 1954, after heavy rains, juveniles dispersing from breeding ponds were in a wide variety of situations, including most of the habitat types represented on the Reservation. Along a small dry gully in an eroded field formerly cultivated, and reverted to tall grass prairie (big bluestem, little bluestem, switch grass, Indian grass), the frogs were numerous. Many of them were flushed by my footsteps from cracks in the soil along the gully banks. In reaching this area the frogs had moved up a wooded slope from the pond, crossed the limestone outcrop area at the hilltop edge, and wandered away from the woods and rocks, out into the prairie habitat. In this prairie habitat there were no rocks providing hiding places at the soil surface, but burrows of the vole (*Microtus ochrogaster*) and other small rodents provided an abundance of subterranean shelter. In the summer of 1955 the frogs were seen frequently in this same area, especially when the soil was wet from recent rain. When the surface of the soil was dry, none could be found and presumably all stayed in deep cracks and burrows.

Anderson (1954: 17) indicated that *G. carolinensis* in Louisiana likewise occurs in diverse habitats, being sufficiently adaptable to satisfy its basic requirements in various ways.

BEHAVIOR

Ordinarily the ant-eating frog stays beneath the soil surface, in cracks or holes or beneath rocks. Probably it obtains its food in such situations, and rarely wanders on the surface. The occasional individuals found moving about above ground are in most instances flushed from their shelters by the vibrations of the observer's footsteps. On numerous occasions I have noticed individuals, startled by nearby footfalls, dart from cracks or under rocks and scuttle away in search of other shelter. Such behavior suggests that digging predators may be important natural enemies. The gait is a combination of running and short hops that are usually only an inch or two in length. The flat pointed head seems to be in contact with the ground or very near to it as the animal moves about rapidly and erratically. The frog has a proclivity for squeezing into holes and cracks, or beneath objects on the ground. The burst of activity by one that is startled lasts for only a few seconds. Then the frog stops abruptly, usually concealed wholly or in part by some object. Having stopped it tends to rely on concealment for protection and may allow close approach before it flushes again.

Less frequently, undisturbed individuals have been seen wandering on the soil surface. Such wandering occurs chiefly at night. Diurnal wandering may occur in relatively cool weather when night temperatures are too low for the frogs to be active. Wandering above ground is limited to times when the soil and vegetation are wet, mainly during heavy rains and immediately afterward.

Pitfalls made from gallon cans buried in the ground with tops open and flush with the soil surface were installed in 1949 in several places along hilltop rock outcrops where the frogs were abundant. The number of frogs caught from day to day under varying weather-conditions provided evidence as to the factors controlling surface activity. After nights of unusually heavy rainfall, a dozen frogs, or even several dozen, might be found in each of the more productive pitfalls. A few more might be caught on the following night, and occasional stragglers as long as the soil remained damp with heavy dew. Activity is greatest on hot summer nights. Below 20° C. there is little surface activity but individuals that had body temperatures as low as 16° C. have been found moving about.

Frogs uncovered in their hiding places beneath flat rocks often remained motionless depending on concealment for protection, but if further disturbed, they made off with the running and hopping gait already described. Although they were not swift, they were elusive because of their sudden changes of direction and the ease with which they found shelter. When actually grasped, a frog would struggle only momentarily, then would become limp with its legs extended. The viscous dermal secretions copiously produced by a frog being handled made the animal so slippery that after a few seconds it might slide from the captor's grasp, and always was quick to escape when such an opportunity was presented.

TEMPERATURE RELATIONSHIPS

Ant-eating frogs are active over a temperature range of at least 16° C. to 37.6° C. They tolerate high temperatures that would be lethal to many other kinds of amphibians, but are more sensitive to low temperatures than any of the other local species, and as a result their seasonal schedule resembles that of the larger lizards and snakes more than those of other local amphibians. The latter become active earlier in the spring.

Earliest recorded dates when the frogs were found active in the course of the present study from 1950 to 1955 were in April every year; the 20th, 25th, 24th, 2nd, 25th, and 21st. Latest dates when the frogs were found in the six years of the study were: October 22, 1949; October 13, 1950; October 7, 1951; August 24, 1952; August 18, 1953; and October 27, 1954 (excluding two late stragglers caught in a pitfall on December 5). Severe drought caused unseasonably early retirement in 1952 and 1953.

Body temperatures of the frogs were taken with a small mercury thermometer of the type described by Bogert (1949: 197); the bulb was used to force open the mouth and was thrust down the gullet into the stomach. To prevent conduction of heat from the hand, the frog was held down through several layers of cloth, at the spot where it was discovered, until the temperature reading could be made. This required approximately five seconds.

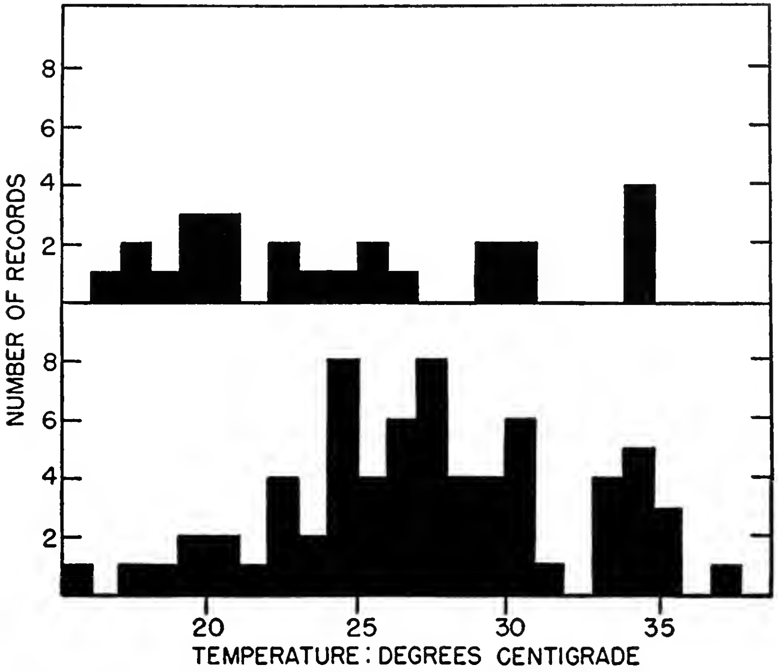

Fig. 1. Temperatures of ant-eating frogs grouped in one-degree intervals; upper figure is of frogs found active in the open, and lower is of those found under shelter. The frogs are active over a temperature range of more than 20 degrees, and show no clear cut preference within this range.

Most of the 79 frogs of which temperatures were measured, were found under shelter, chiefly beneath flat rocks. The rocks most utilized were in open situations, exposed to sunshine. Most of the frogs were in contact with the warmed undersurfaces of such rocks. Forty-three of the frogs, approximately 54.5 percent, were in the eight-degree range between 24° and 31° C. Probably the preferred temperatures lie within this range. The highest body temperature recorded, 37.6° C., was in a frog which "froze" and remained motionless in the sunshine for half a minute after the rock sheltering it was overturned. Probably its temperature was several degrees lower while it was sheltered by the rock. Other unusually high temperatures were recorded in newly metamorphosed frogs found hiding in piles of decaying vegetation near the edge of the pond, on hot afternoons of late August. Temperatures ranged from 17.0° to 30.7° in frogs that were found actually moving about. Several with relatively low temperatures, 22° to 17°, were juveniles travelling in rain or mist on cool days. These frogs, having relatively low temperature, were sluggish in their movements, as compared with individuals at the upper end of the temperature range.

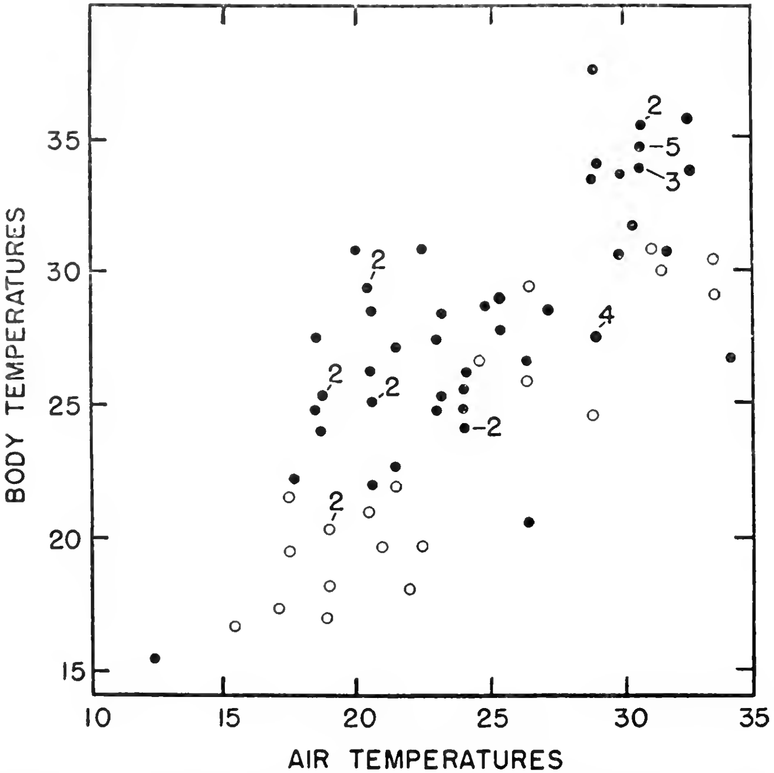

FIG. 2. Body temperatures and nearby air temperatures for frogs found under natural conditions. Dots represent frogs found under shelter; circles represent those found in the open.

After the first frost each year the frogs usually could not be found, either in the open or in their usual hiding places beneath rocks. They probably had retired to deep subterranean hibernation sites. The only exception was in 1954, when two immature frogs were found together in a pitfall on the morning of December 5 after a rain of .55 inches ending many weeks of drought. Air temperature had been little above 10° C. that night, but had often been below freezing in the preceding five weeks.

Reactions of these same two individuals to low temperatures were tested in the laboratory. At a body temperature of 11° C. they were extremely sluggish. They were capable of slow, waddling movements, but were reluctant to move and tended to crouch motionless. Even when they were prodded, they usually did not move away, but merely flinched slightly. At 6° C. they were even more sluggish, and seemed incapable of locomotion, as they could not be induced to hop or walk by prodding with a fine wire. When placed upside down on a flat surface, they could turn over, but did so slowly, sometimes only after a minute or more had elapsed. Respiratory throat movements numbered 46 and 60 per minute.

BREEDING

Many observers have noted that breeding activity is initiated by heavy rains in summer. In my experience precipitation of at least two inches within a few days is necessary to bring forth large breeding choruses. With smaller amounts of precipitation only stragglers or small aggregations are present at the breeding ponds. Tanner (1950: 48) stated that in three years of observation, near Lawrence, Kansas, the first storms to bring large numbers of males to the breeding ponds occurred on June 20, 1947, June 18, 1948, and May 1, 1949.

In 1954 the frogs were recorded first on April 25, but these were under massive boulders, and were still semi-torpid. Frogs were found fully active, in numbers, under small flat rocks on May 7. They were found frequently thereafter. On the afternoon of May 13, the third consecutive day with temperature slightly above 21° C., low croaking of a frog was heard among rocks at an old abandoned quarry. Throughout the remainder of May, calling was heard frequently at the quarry on warm, sunny afternoons. Often several were calling within an area of a few square yards, answering each other and maintaining a regular sequence. In the last week of May rains were frequent, and the precipitation totalled 2.09 inches. On June 1 and 2 also, there were heavy rains totalling 2.26 inches. On the evening of June 2 many frogs were calling at a pond ½ mile south of the Reservation, and one was heard at the pond on the Reservation. By the evening of June 4, dozens were calling in shallow water along the edge of this pond in dense *Polygonum* and other weeds. There was sporadic calling even in daylight and there was a great chorus each evening for the next few days, but its volume rapidly diminished.

In mid-June a system of drift fences and funnel traps was installed 200 yards west of the pond in the dry bottom of an old diversion ditch leading from the pond. The ditch constituted the boundary between bottomland pasture and a wooded slope, and therefore was a natural travelway. The object of the installation was to intercept and catch small animals travelling along the ditch bottom. The drift fence was W-shaped, with a funnel trap at the apex of each cone so that the animals travelling in either direction would be caught. The numbers of frogs caught from time to time during the summer provided information as to their responses to weather in migrating to the pond.

TABLE 1. NUMBERS OF FROGS CAUGHT WITHIN TWO DAYS AFTER RAIN IN FUNNEL TRAPS IN 1954, FROM MID-JUNE, TO THE TIME OF FIRST FROST.

Date	Precipitation in inches	No. of caught frogs
July 1	2.02	8
July 10	.11	none
July 16	1.26	none
July 20-21	.94	3
July 24	.38	2
July 28	.29	none
August 1-2	3.22	31
August 6-7-8	2.43	none
August 12	.28	none
August 16	.29	none
August 19-22	.70	none
August 27-28	1.05	none
September 9	.50	none
September 29-30	.38	none
October 4	.74	none
October 12-14	3.51	none

From the positions of the traps and drift fences, it was obvious that all of the frogs that were caught were travelling toward the pond. Capture of an equal number moving away from the pond a few days afterward might have been expected but none at all was caught while making a return trip. Therefore it seems that the frogs returned by a different route to their home ranges after breeding. Of necessity they make the return trip under conditions drier than those that prevail on the pondward trip, which is usually made in a downpour. Probably the return travel is slower, more leisurely, and with more tendency to keep to sheltered situations.

The call is a bleat, resembling that of a sheep, but higher, of lesser volume, and is not unlike the loud rattling buzz of an angry bee. The call is usually of three to four seconds duration, with an interval several times as long. Calling males were floating, almost upright, in the water within a few yards of shore, where there was dense vegetation. The throat pouch when fully expanded is several times as large as the entire head. When a person approached to within a few yards of frogs they usually stopped calling, submerged, and swam to a place of concealment.

Having heard the call of typical *G. carolinensis* in Louisiana, I have the impression that it is a little shorter, more sheeplike, and less insectlike than that of *G. olivacea.* The call of *Gastrophryne* is of such peculiar quality that it is difficult to describe. Different observers have described it in different terms. Stebbins (1951: 391) has described the call in greatest detail, and also has quoted from the descriptions of it previously published. These descriptions include the following: "high, shrill buzz"; "buzz, harsh and metallic"; "like an electric buzzer"; "like bees at close range but more like sheep at a distance"; "bleating baa"; "shrill, long-drawn quaw quaw"; "whistled whēē followed by a bleat."

Stebbins observed breeding choruses (*mazatlanensis*) at Peña Blanca Springs, Arizona, and stated that sometimes three or four called more or less together, but that they seldom started simultaneously. Occasionally many voices would be heard in unison followed by an interval of silence, but this performance was erratic. At the pond on the Reservation I noted this same tendency many times. After a lull the chorus would begin with a few sporadic croaks, then four or five or even more frogs would be calling simultaneously from an area of a few square yards. Anderson (*op. cit.:* 34) found that in small groups of calling *G. carolinensis* there was a distinct tendency to maintain a definite pattern in the sequence of the calls. One "dominant" individual would initiate a series of calls, and others each in turn would take up the chorus.

Pairing takes place soon after the breeding aggregations are formed. On the night of June 4, 1954, a clasping pair was captured and kept in the laboratory in a large jar of water. This pair did not separate, and spawning occurred between noon and 1:30 P. M. on June 5. When the newly laid eggs were discovered at 1:30 P. M. most of them were in a surface film. Some were attached to submerged leaves and a few rested on the bottom. The pair was still joined, but the male was actually clasping only part of the time, and as the frogs moved about in the water, it became evident that they were adhering to each other by the areas of skin contact, which were glued together by their dermal secretion. They were unable to separate immediately, even when they struggled to do so. They were observed for approximately 15 minutes before separation occurred, and during this time they were moving about actively. As they separated, the area of adhesion was discernible on the back of the female. It was U-shaped, following the ridges of the ilia and the sacrum.

On August 2, 1954, after a rain of 3.22 inches, the previously mentioned funnel trap in the ditch had caught 31 ant-eating frogs. Water had collected to a depth of several inches in the depression where the trap was situated. A dozen of the trapped frogs were clasping pairs. These frogs struggled vigorously as they were removed from the traps, handled and marked. As a result most of the clasping males were separated from the females. In handling those of each pair I noticed that they were glued together by dermal secretions, as were those of the pair observed on June 5. The areas of adhesion were of similar shape and location in the different pairs, and included the U-shaped ridge of the female's back and the male's belly, and the inner surfaces of the male's forelegs with the corresponding surfaces of the female's sides where the male clasped.

This adhesion of the members of a pair during mating may be a normal occurrence. The copious secretion of the dermal glands is of especially glutinous quality in *Gastrophryne*. The adhesion of members of a pair may have survival value. These small frogs are especially shy, and in the breeding ponds they respond to any disturbance with vigorous attempts to escape and hide. Under such circumstances the adhesion may prevent separation. Also, it may serve to prevent displacement of a clasping male by a rival. Anderson (*op. cit.*) who observed many details of the mating behavior of *G. carolinensis*, both in the laboratory and under natural conditions, mentioned no such adhesion between members of a pair.

Anderson (*op. cit.*: 31) discussed the possibility that reproductive isolation might arise in sympatric populations, such as those of *G. carolinensis* in southern Louisiana, through inherent differences in time of spawning. However, in *G. olivacea* at least, such isolation would be prevented by individual males returning to breed at different times in the same season. Furthermore, individual differences in choice of breeding time probably result from environmental factors rather than genetic factors in most instances. In *G. olivacea* in Kansas, time of breeding is controlled by the distribution of heavy rainfall creating favorable conditions. Onset of the breeding season may be hastened or delayed, or an entire year may be missed because of summer drought. If favorable heavy rains are well distributed throughout the summer, frogs of age classes that are not yet sexually mature in the early part of the breeding season, may comprise the bulk of the breeding population in late summer.

DEVELOPMENT OF EGGS AND LARVAE

Eggs laid on June 5 by the pair kept in the laboratory were hatching on June 7, on the average approximately 48 hours from the time of laying. By June 8 all the eggs had hatched and the tadpoles were active. On August 28 and 29 thousands of newly metamorphosed young were in evidence on wet soil at the pond margin; in some the head still was tadpolelike and they had a vestige of the tail stump. These young were remarkably uniform in size, 15 to 16 mm. (the smallest one found was 14½ mm.) and almost all of them had originated from eggs laid after heavy precipitation, totalling 3.22 inches, in the first 36 hours of August. Allowing one day for adults to reach the pond and spawn, and two days more for eggs to hatch, the tadpole stage must have lasted approximately 24 days in this crop of young.

Wright and Wright (1949: 582) stated that the tadpoles metamorphosed after 30 to 50 days, and that the newly metamorphosed frogs are 10 to 12 mm. in length. Length of time required for larval development probably varies a great deal depending on the interaction of several factors such as temperature and food supply.

GROWTH

Little has been recorded concerning the growth rate of *Gastrophryne* or the time required for it to attain sexual maturity. Wright (1932) found that *G. carolinensis* in the Okefinokee Swamp region has a mean metamorphosing-size of 10.8 mm. Young thought to be those recently emerged from their first hibernation were those in the size group 15.0 to 20.0 mm., while the frogs in the 20 to 27 mm. size class and those in the 27 to 36 mm. class were interpreted as representing two successivly older annual age classes. Anderson (1954: 41) thought he could recognize four successive annual age classes in the same species in southern Louisiana. He found that sexual maturity is attained at a length of 21 to 24 mm. in frogs which he believed to be late in the second year of life.

Allowing for size differences between the two species, Wright's and Anderson's conclusions regarding growth in *G. carolinensis,* on the basis of size groups, are largely substantiated by my own data on the growth of marked individuals of *G. olivacea* living under natural conditions in Kansas.

In 1954, an opportunity to investigate the early growth was afforded by unusually favorable circumstances. The population of frogs that emerged from hibernation in the late spring of 1954 included few, if any, that were below adult size; drought had prevented successful breeding in 1952 and 1953. Heavy rains in the first week of June, 1954, and again in the first week of August, resulted in the production of two successive crops of young so widely spaced that they were easily distinguishable. Some young may have been hatched after other minor rains, but certainly these were relatively few. Young from the eggs laid in the first week of August were metamorphosing during the last week of August. Growth in the frogs of this group can be shown by the average size and the size range of the successive samples collected.

TABLE 2. GROWTH IN FROGS METAMORPHOSED IN THE LAST WEEK OF AUGUST, 1954.

Time of sample	Number in sample	Mean size in mm.	Size range in mm.
August 27 to 31	27	15.55 ± .079	15 to 17
September 11	114	17.2 ± .033	14 to 20
September 15 to 22	12	18.7 ± .090	16 to 20
September 27 to 30	37	19.3 ± .055	17 to 21.5
October 1 to 7	62	20.8 ± .072	17 to 24
October 12 to 17	49	22.3 ± .092	18 to 24

By mid-October, six weeks after metamorphosis, these frogs had increased in over-all length by approximately 50 percent. Having grown a little more than 1 mm. per week on the average, they were approximately intermediate in size between small adults and newly metamorphosed young.

The frogs hatched in June were present in relatively small numbers compared with those hatched in August, and were not observed metamorphosing. In late August a sample of 33 judged to belong to the June brood averaged 26.2 (22-28) mm. long. A sample of 39 from the first week of October averaged 28.1 (24.5-32) mm. Frogs of this group thus were approaching small adult size late in their first growing season. Such individuals possibly breed in the summer following their first hibernation, when they are a year old or a little more. Because recaptured frogs were not sacrificed to determine the state of their gonads, the minimum time required to attain sexual maturity was not definitely determined. The available evidence indicates that sexual maturity is most often attained late in the second year of life, at an age of approximately two years. The darkened and distensible throat pouch of the adult male probably is the best available indicator of sexual maturity.

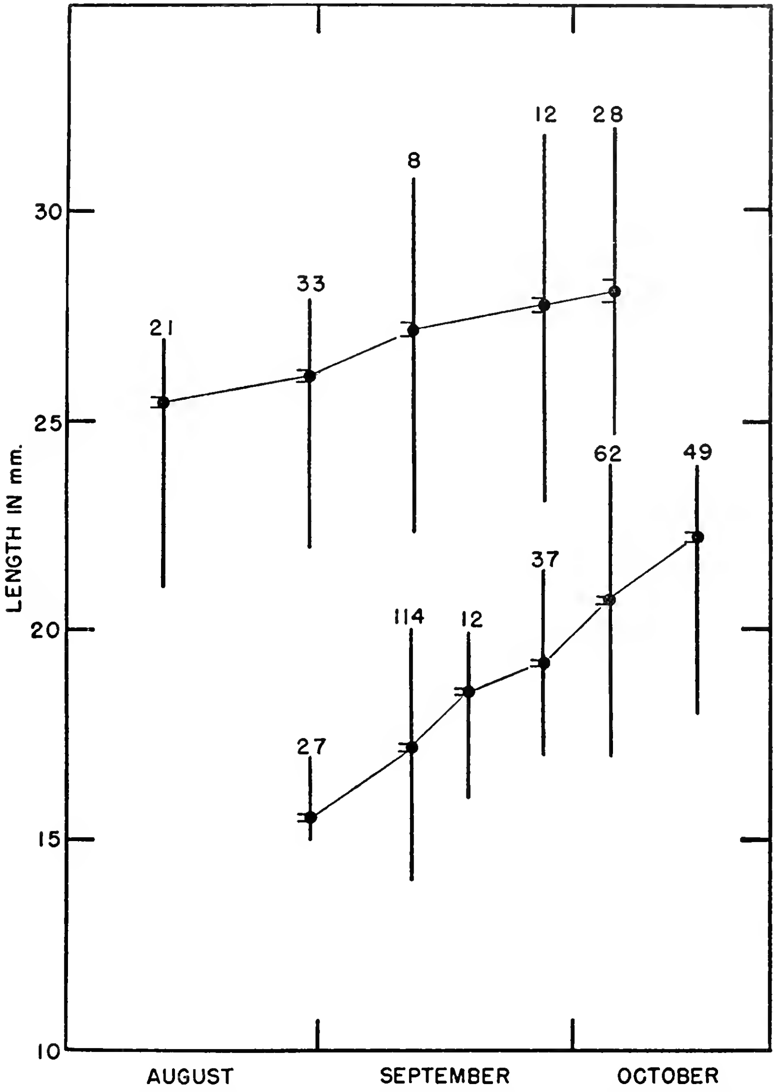

FIG. 3. Growth shown by successive samples of young ant-eating frogs of two size groups in late summer and early fall of 1954. For each sample the mean, standard deviation, and range are shown. Lower series are those metamorphosed in late August, and upper series are those metamorphosed in late June.

Frogs that metamorphose in late summer have little time to grow before hibernating, and still are small when they emerge in spring. The smallest one found was 19 mm. long (May 19, 1951), and in each year except 1954 many such young were found that were less than 25 mm. in length in May or early June. None of the frogs marked at or near metamorphosing size has been recaptured, but the trend of early growth is well shown by Table 2 and Fig. 3. However, many juveniles that were captured and marked within a few weeks of metamorphosis were recaptured as adults. The selected individuals in Table 3 are considered typical of growth from "half-grown" to small adult size. Growth in many other individuals is shown in Figs. 6 and 7.

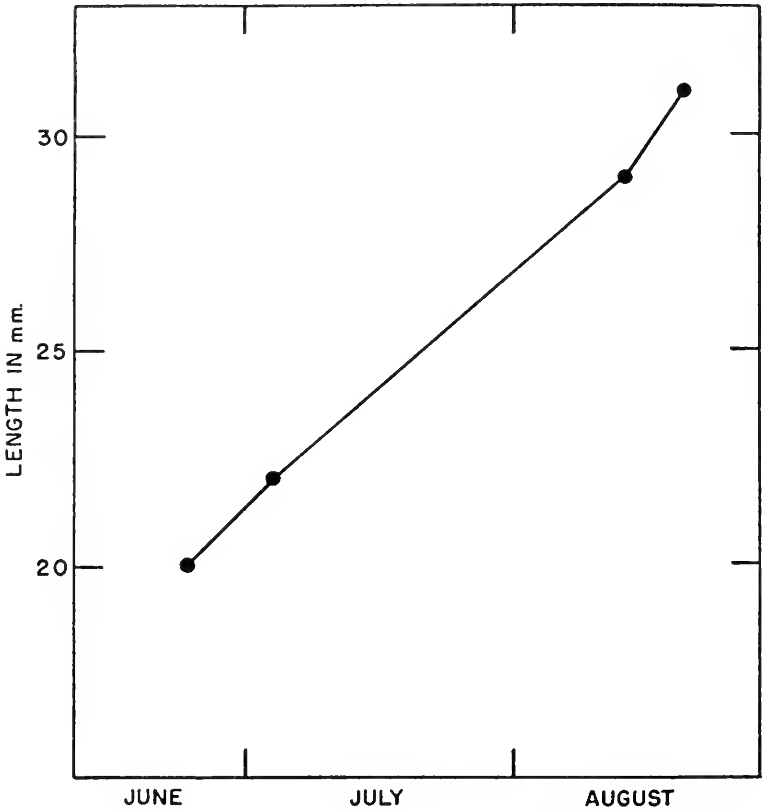

FIG. 4. Rapid growth of a young female caught in June, July, and August, 1949. Presumably this individual metamorphosed late in the summer of 1948, and at the age of approximately one year it was near small adult size.

TABLE 3. GROWTH IN FROGS MARKED AS YOUNG AND RECAPTURED AS SMALL ADULTS.

Individual and sex	Dates of capture	Length in mm.	Probable time of metamorphosis
No. 1 ♀	August 28, 1951	21.5	Mid-July, 1951
	May 5, 1952	23	
	July 3, 1952	32	
	August 31, 1952	33	
No. 2 ♀	June 8, 1950	25	Late July, 1949
	May 24, 1951	31	
	July 30, 1951	34	
	June 24, 1952	35	
No. 3 ♂	August 31, 1951	24	Late June, 1951
	May 23, 1953	32	

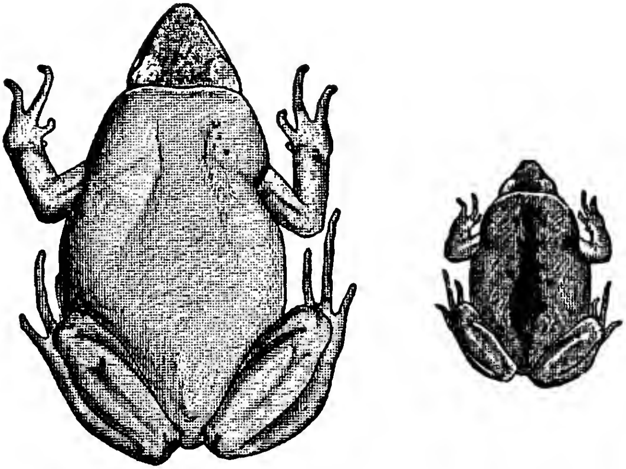

FIG. 5. Ant-eating frogs, a little less than twice natural size, adult and newly metamorphosed young, showing differences in size and coloration. The young is darker and has a leaflike middorsal mark which fades as growth proceeds.

The trend of growth after attainment of minimum adult size is also well shown by the records of marked individuals recaptured. Many of these were marked while they were still small so that their approximate ages are known. For those recaptured in their second year, after one hibernation, length averaged 30.92 mm. Some of this group were young metamorphosed late the preceding summer and still far short of adult size (as small as 23 mm.) when recaptured. Others were relatively large, up to 33 mm. A group of 22 recaptured frogs known to be in their third year averaged 33.3 mm. (males 31.9, females 35.3, excluding four individuals of undetermined sex). Fifteen other recaptured frogs were known to be in their fourth year at least, and some probably were older, as they were already large adults when first examined. These 15 averaged 36.6 mm. (males 34.7, females 37.9 mm.). Size was similar in a sample of 58 individuals intercepted en route to the breeding pond in heavy rains of June and August, 1954. The 38 males in this sample ranged in size from 30 mm. to 38 mm., averaging 34.5. The 20 females ranged from 34 mm. to 40 mm., averaging 37.65. The large average and maximum size in this sample of a breeding population may be typical after periods of drought years have prevented successful reproduction. Summer drought in 1952 and 1953 prevented breeding in those years, or, at least, it drastically reduced the numbers of young produced. One-year-old and two-year-old frogs may not have been represented at all in the sample of 58. Three-year-old frogs presumably made up a substantial part of the sample, since 1951 was a year of successful breeding.

Differences in size between species and geographic variation in size in *Gastrophryne* have been given little attention by herpetologists, but if understood, would help to clarify relationships. Hecht

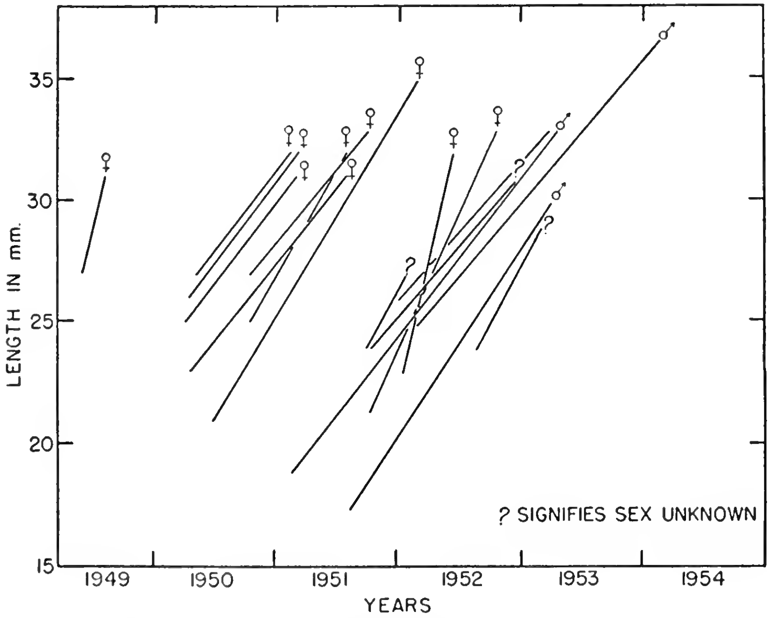

FIG. 6. Growth in a group of frogs, each marked while still short of adult size and mostly recaptured after lapse of one or more hibernation periods. Each line connects records of an individual frog.

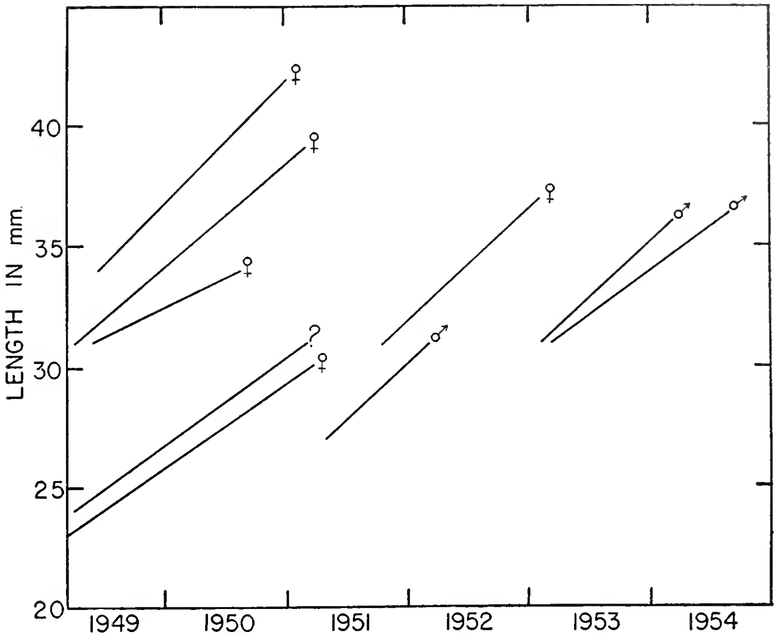

FIG. 7. Growth in another group of frogs that were marked as young or small adults and recaptured after intervals of more than a year. Frogs of this group were, on the average, larger than the individuals shown in Fig. 6, and they made less rapid growth.

and Matalas stated in their revision (1946: 5) that size is of no importance as a taxonomic character, as typical *carolinensis, olivacea,* and *mazatlanensis* all averaged approximately the same—26 to 28 mm.—females slightly larger than males. However, they arbitrarily classed as adults all individuals 22.5 mm. in length or larger, having found individuals this small that showed the darkened and distensible throat pouches characteristic of adult males. From the trend of my own measurements of G. *olivacea* in northeastern Kansas, I conclude that either many immature individuals were included in their samples, or that the populations sampled included some with individuals that were remarkably small as adults.

The population which I studied may be considered typical of G. *olivacea.* They averaged large, including individuals up to 42 mm. in length, well above the maximum sizes for any reported in the literature. At metamorphosis these *olivacea* are of approximately 50 percent greater length than G. *carolinensis* as reported by Wright and Wright (1949: 573) and Anderson (1954: 41). Yet Blair (1950: 152) observed that in eastern Oklahoma, where the ranges of *olivacea* and *carolinensis* overlap, the latter is larger. On the basis of field and laboratory observations he tentatively concluded that one of the main barriers to interbreeding was the reluctance of the males of *carolinensis* to clasp the smaller females of *olivacea*.

That size differs in different populations, and is still poorly understood, is illustrated by the following discrepant figures from various authors.

TABLE 4. SIZE RANGE OF ADULTS IN VARIOUS POPULATIONS OF GASTROPHRYNE.

Species or subspecies	Geographic population sampled	Authority	Size range of adults in mm.
olivacea	Douglas Co., Kansas	present study	31 to 42
olivacea	entire range	Wright and Wright (1949)	19 to 38
carolinensis	entire range	Wright and Wright (1949)	20 to 36
carolinensis	southern Louisiana	Anderson (1954)	22 to 35
areolata	southeastern Texas	Wright and Wright (1949)	23 to 29
mazatlanensis	Arizona and New Mexico	Wright and Wright (1949)	22 to 30
mazatlanensis	Santa Cruz Co., Arizona	Stebbins (1951)	25.2 to 31.5

COLOR AND PATTERN

The color pattern changes in the course of development, and the shade of color changes in response to environmental conditions. At the time of metamorphosis, young are dark brown with specks of black and with a dark, cuneate, leaflike middorsal mark. The narrow end of this mark arises just behind the head, and the mark extends posteriorly as far as the hind leg insertions. At its widest, the mark covers about half the width of the dorsal surface. The lateral edges of the mark are sharply defined, but at its anterior and posterior ends it blends into the ground color. In most individuals smaller than 20 mm., this dorsal mark is well defined and conspicuous. As growth proceeds, however, it becomes faint. In frogs 19 to 25 mm. long the marks have disappeared. In individuals of this size the brown ground color is markedly paler than in those newly metamorphosed, but is darker than in adults.

In large adults the dorsal coloration is a uniform pale tan, paler on the average in females than in males. Temperature and moisture both affect the shade of coloration. In frogs that were partly desiccated, the color was unusually pale, with a distinctly greenish tint, and at high temperatures coloration tended to be relatively pale.

Hecht and Matalas (1946) have described and figured color patterns in various populations of *Gastrophryne*, demonstrating geographic trends and helping to clarify relationships. Their account indicates that the dark dorsal mark present in young of *olivacea* but not present in adults, is better developed and longer persisting in other forms. Specimens of *carolinensis*, presumably adult, are figured which have the dark middorsal area contrasting with paler color of the sides. The dark area is seen to consist of dots or blotches of black pigment which may be in contact producing more or less continuous black areas, or may be separate and distinct producing a spotted pattern. Pigmentation is usually most intense along the lateral edges of the dorsal leaflike mark; the central portion may be so much paler that the effect is that of a pair of dorsolateral stripes. This latter type of pattern is best developed in the population of Key West, Florida. Hecht and Matalas did not consider these insular frogs to be taxonomically distinct, because only 48 per cent of specimens from the Florida keys had the "Key West" pattern, while 29 per cent resembled *olivacea* and 23 per cent resembled *carolinensis*. In the southwestern subspecies (or species) *mazatlanensis*, recorded from several localities in Sonora and from extreme southern Arizona, the dorsal pigmentation similarly tends to be concentrated in dorsolateral bands, but is much reduced or almost absent, and there is corresponding pigmentation dorsally across the middle of the thigh, across the middle of the shank, and on the foot. When the leg is folded, these three dark areas are brought in contact with each other and with the dorsolateral body mark, if it is present, to form a continuous dark area, in a characteristic "ruptive" pattern. Hecht and Matalas found similar leg bars, less well developed, in certain specimens of *olivacea* including one from Gage County, Nebraska, at the northern end of the known geographic range.

MOVEMENTS

Freiburg (*op. cit.*: 384) concluded that ant-eating frogs seem to have no individual home ranges, but wander in any direction where suitable habitat is present. However, from records covering a much longer span of time, it became increasingly evident that a frog ordinarily tends to stay within a small area, familiar to it and providing its habitat requirements.

Nevertheless, in all but a few instances the marked frogs recaptured were in new locations a greater or lesser distance from the site of original capture. The movements made by these frogs were of several distinct types:

1. Routine day to day movements from shelter to shelter within the area familiar to the animal, the "home range."
2. Shifts from one home range to another; such shifts may have been either long or short, and may have occurred abruptly or by gradual stages.
3. Travel by adults to or from a breeding pond. In most or all instances these adults were regularly established in permanent home ranges, and they often moved through areas unsuitable as habitat to reach the ponds.
4. Movements of dispersal in the young, recently metamorphosed and not yet settled in a regular home range.

Usually there was uncertainty as to which types of movements had been made by the recaptured individuals. Some may have made two or three different types of movements in the interval between captures.

On many occasions individuals were found beneath the same rock on two consecutive days, or occasionally on several successive days. Rarely, such continued occupancy of a niche lasted several weeks. In 1949, a frog was found under the same rock on June 4, 6, 26, 27, and July 1, 3 and 11. This was an immature female, presumably metamorphosed late in the summer of 1948. During the five weeks period covered by the records, it grew from 27 mm. to 34 mm. In 1952, another individual was found under its home rock on June 23 and 30, July 2 and 3, and August 14 and 20. In 1952 a juvenile was found under a rock on May 30, June 4, and June 17. These three individuals were exceptional in their continued occupancy of the same niches. Among the hundreds of others recorded, none was found more than twice in any one place.

Despite the fact that field work was concentrated on small areas which were worked intensively, only eight per cent of the frogs recorded were ever recaptured, and most of those were recaptured only once. Only 13 individuals yielded series of records, well spaced, in two or more different years. These few individuals recaptured frequently may not be typical of the entire population. The low incidence of recaptures indicates that relatively few of the frogs present on an area at any one time have been taken. Because of their secretive and subterranean habits most of the frogs are missed by a collector who searches by turning rocks, or trapping with pitfalls. Therefore, even though a marked frog may survive and remain within a radius of a few hundred feet of one point for months or even years, the chances of recapture are poor.

One female was caught first as a juvenile on June 8, 1950. On April 24, 1951, when first recaptured, she had grown to small adult size, and was only 18 feet from the original location. On July 30, 1951, however, she was recaptured 750 feet away. At a fourth capture on May 21, 1952, she had shifted 70 feet farther in the same direction. At the final capture on June 24, 1952, she was approximately 140 feet from both the third and fourth locations. The sequence of these records suggests that the frog had already settled in a home range at the time of her first capture in 1950, and that approximately a year later she shifted to a second home range, which was occupied for the following year, at least.

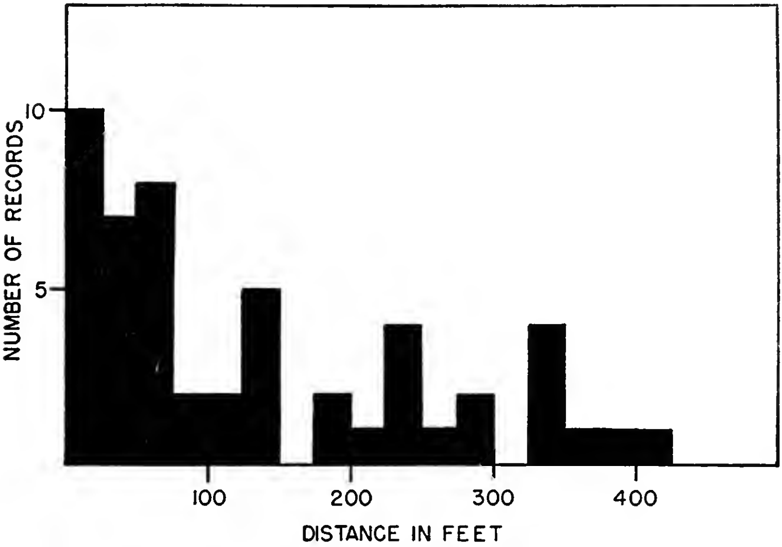

FIG. 8. Distances between captures in frogs marked, and recaptured after substantial intervals including one or more hibernations. Distances are grouped in 25-foot intervals. For longer distances the trend is toward progressively fewer records, indicating that typical home ranges are small.

In several instances, after recaptures as far as 400 feet from the original location, frogs were again captured near an original location, suggesting that for some individuals, at least, home ranges may be as much as 400 feet in diameter.

Figure 8 shows that for movements of up to 400 feet, numbers of individuals gradually decrease with greater distance. For distances of more than 400 feet there are comparatively few records. Of the 59 individuals recaptured after one or more hibernations, only nine had moved more than 400 feet from the original location. Twenty-five were recaptured at distances of 75 feet or less. The mean distance for movement for all individuals recaptured was 72 feet. A typical home range, therefore, seems to average no more than 75 feet in radius. Of the 59 individuals recaptured after one or more hibernations, 47 were adults and probably many of these had made round-trip migrations to the breeding pond. This was not actually demonstrated for any one individual, but several were captured in each of three or four different years near the same location.

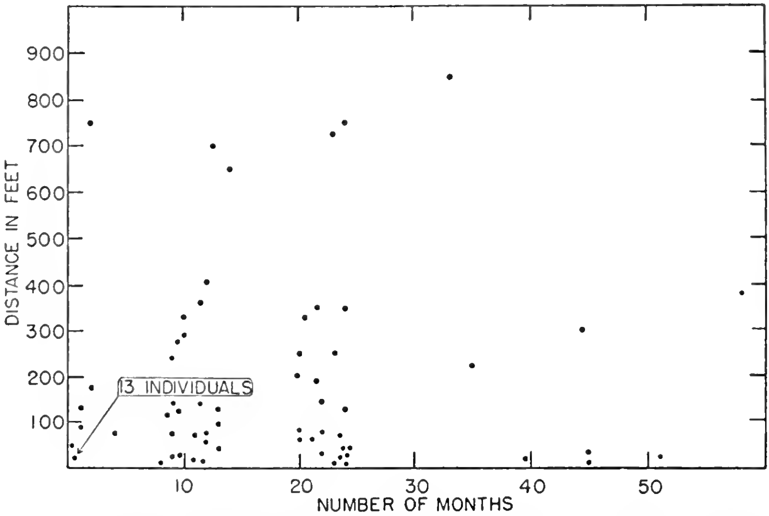

FIG. 9. Distances between captures and elapsed time in months in marked frogs recaptured. Few records are for distances more than 400 feet. There is but little tendency to longer movements in those caught after relatively long intervals.

The trend of movements differed in the sexes. Males are more vagile. Of 21 adult males recaptured, none was less than 40 feet from its original location, whereas six of the 26 adult females were less than 40 feet away from the original point of capture. Of seven frogs that had wandered 700 feet or more, five were males.

FOOD HABITS

According to Smith (1934: 503) stomachs of many specimens, from widely scattered localities in Kansas, contained only large numbers of small ants. Tanner (1950: 47) described the situation of a frog found on the Reservation buried in loose soil beneath a flat rock, beside an ant burrow, where, presumably, the frog could snap up the passing ants without shifting its position. Anderson (*op. cit.*: 21) examined alimentary tracts of 203 specimens of *carolinensis* from Louisiana, representing a year round sample for several different habitats. He found a variety of small animals including ants, termites, beetles, springtails, bugs, ear-wigs, lepidopterans, spiders, mites, centipedes, and snails. Most of these prey animals were represented by few individuals, and ants were much more numerous than any of the other groups. Anderson concluded that ants, termites, and small beetles were the principal foods. He noted that some of the beetles were of groups commonly found in ant colonies. Tanner reported that in a large number of the frogs which he collected in Douglas, Riley, Pottawatomie, and Geary counties, Kansas, the digestive tracts and feces contained only ants. Wood (1948: 226) reported an individual of *G. carolinensis* in Tennessee found under a flat rock in the center of an ant nest.

Freiburg (*op. cit.*: 383) reported on the stomach contents of 52 ant-eating frogs collected near the Reservation. Ants constituted nearly all these stomach contents, though remains of a few small beetles were found. The ants eaten were of two kinds, *Lasius interjectus* and *Crematogaster* sp. The latter was by far the more numerous.

Although I made no further study of stomach contents, the myrmecophagous habits of *Gastrophryne* have come to my attention frequently in the course of routine field work. Individuals kept in confinement for a day or more almost invariably voided feces which consisted mainly or entirely of ant remains, chiefly the heads, as these are most resistant to digestion.

Often upon examining frogs I have found ants (*Crematogaster* sp.) or their severed heads, attached with mandibles embedded in the skin. To have been attacked by ants, the frogs must have been in or beside the ants' burrow systems. Frequently the frogs that were uncovered beneath rocks were adjacent to clusters of ants or to their nests or travelways, in a position strategically located to feed upon them, as described by Tanner. Often the feces of the frogs were found in pitfalls or under flat rocks. Although these feces were not analyzed, they seemed to consist mainly or entirely of ant remains.

The species of *Crematogaster*, which is the chief food of *Gastrophryne* in this region, is largely subterranean in habits, and is extremely abundant. Any flat rock in damp soil is likely to harbor a colony beneath it. Colonies are situated also in damp soil away from rocks, beneath almost any kind of debris, and in hollow weed stalks and decaying wood. Live-traps for small mammals, having nest boxes attached, almost always were occupied by colonies of *Crematogaster*, if they were left in the field in warm, humid weather. Occasionally the ants attacked and killed small mammals caught in such traps. Among the thousands of kinds of insects occurring on the Reservation, this ant is one of the most numerous in individuals, one of the most important on the basis of biomass and provides an abundant food source for those predators that are ant eaters. Food supply probably is not a limiting factor to populations of *Gastrophryne* on the area.

PREDATION

Young copperheads are known to feed upon ant-eating frogs occasionally (Anderson, 1942: 216; Freiburg, 1951: 378). Other kinds of snakes supposedly eat them also. The common water snake (*Natrix sipedon*) and garter snake (*Thamnophis sirtalis*) probably take heavy toll of the adults at the time they are concentrated at the breeding pools. Larger salientians may be among the more important enemies of the breeding adults, the tadpoles, and the newly metamorphosed young. Bullfrogs (*Rana catesbeiana*) and leopard frogs (*Rana pipiens*) are normally abundant at the pond on the Reservation. These large voracious frogs lining the banks are quick to lunge at any moving object, and must take heavy toll of the much smaller ant-eating frogs that have to pass through their ranks to reach the water. The newly metamorphosed young often are forced to remain at a pond's edge for many days, or even for weeks, by drought and they must be subject to especially heavy predation by ranid frogs. Even the smallest newly metamorphosed bullfrogs and leopard frogs would be large enough to catch and eat them.

As a result of persistent drought conditions in 1952 and 1953, bullfrogs were completely eliminated from the pond by early 1954. Re-invasion by a few individuals occurred in the course of the summer; these probably made long overland trips from ponds or streams that had persisted through the drought. Leopard frogs reached the pond in somewhat larger numbers, but their population in 1954 was only a small percentage of that present in most other years. Notable success in the ant-eating frog's reproduction in 1954 may have been due largely to the scarcity of these large ranids at the breeding ponds.

Freiburg (*loc. cit.*) noted that many of the ant-eating frogs he examined were scarred, and some had digits or limbs amputated. He did not speculate concerning the origin of these injuries. However, it seems likely that many or all of them were inflicted by the short-tailed shrew (*Blarina brevicauda*). Five-lined skinks living on the same area were likewise found to be scarred by bites which I identified (Fitch, 1954: 133) as bites of the short-tailed shrew. This shrew is common on the Reservation, especially in woodland. Many have been trapped in the pitfalls. On several occasions when a short-tailed shrew was caught in the same pitfall with ant-eating frogs, it was found to have killed and eaten them. Like the frogs, the shrews were most often caught in pitfalls just after heavy rains. Once in 1954 a shrew was found at the quarry in a pitfall that had been one of those most productive of frogs. The bottom of the pitfall was strewn with the discarded remains (mostly feet and skins) of perhaps a dozen ant-eating frogs. All had been eaten during one night and the following morning, as the trap had been checked on the preceding day. On other occasions shrews caught in pitfalls with several frogs had killed and eaten some and left others unharmed.

SUMMARY

In northeastern Kansas the ant-eating frog, *Gastrophryne olivacea,* is one of the more common species of amphibians. This area is near the northern limits of the species, genus, and famliy. The species prefers a dry, rocky upland habitat often in open woods or at woodland edge where other kinds of salientians do not ordinarily occur. It is, however, tolerant of a wide variety of habitat conditions, and may occur in river flood plains or cultivated land. In these situations where surface rocks are absent, cracks and rodent burrows presumably furnish the subterranean shelter that it requires.

This frog is secretive and spends most of the time in subterranean shelter, obtaining its food there rather than in the open. Only on warm rainy nights is it inclined to venture into the open. Then, it moves about rapidly and with a scuttling gait, a combination of running and short hops. However, it may be flushed in daylight from a hiding place by the vibrations from footsteps of a person or an animal, or it may move about in the daytime when temperatures at night are too low for activity. Though not swift of foot, the frogs are elusive because of their tendency to keep under cover, their slippery dermal secretion, and the ease with which they find and enter holes, or crevices to escape.

Breeding occurs at any time from late May through August and

is controlled by the distribution of rainfall. Heavy precipitation, especially rains of two inches or more, stimulates the frogs to migrate in large numbers to breeding ponds. Even though there are several well spaced periods of unusually heavy rainfall in the course of a summer, each one initiates a new cycle of migration, mating and spawning. Heavy rainfall is a necessity, not only to ensure a water supply in temporary pools where the frogs breed, but to create the moist conditions they require for an overland migration. An individual male may migrate to a pond and breed at least twice in the same season. Whether or not the females do likewise is unknown. Amplexus and spawning occur mainly within a day or two after the frogs reach the ponds. The males call chiefly at night, but there may be daytime choruses when breeding activity is at its peak. Many males concentrate within a few square yards in the choruses and float upright usually beside or beneath a stem or leaf, or other shelter, rendering them extremely inconspicuous. The call is a bleat of three seconds duration, or a little more. In amplexus the members of a pair sometimes become glued together by their viscous dermal secretions. The eggs hatch in approximately 48 hours. The tadpoles metamorphose in as few as 24 days. Newly metamorphosed frogs are 15 to 16 mm. in length, or, rarely as small as 14.5 mm. They are thus much larger than newly metamorphosed *G. carolinensis,* which have been described as 10-12 mm. or even as small as 8.5 mm. The newly metamorphosed frogs disperse from the breeding ponds as soon as there is a heavy rain. The young grow a little more than one mm. in length per week. Those metamorphosed in early summer may attain minimum adult size before hibernation which begins in October. It seems that sexual maturity is most often attained in the second season, at an age of one to two years.

Gastrophryne belongs to a family that is primarily tropical in distribution, and frogs of this genus have much higher temperature thresholds than most other amphibians of northeastern Kansas, with a correspondingly short season of activity. For more than half the year, mid-October to early May the frogs are normally in hibernation. Body temperatures of active frogs ranged from 17.0° C. to 37.6° C., but more than two-thirds were within the relatively narrow range, 24.0° to 31°. Near the date of the first autumn frost the frogs disappear from the soil surface and from their usual shelters near the surface, presumably having retired into hibernation in deep holes and crevices.

The natural enemies include young of the copperhead. The bullfrog and leopard frog probably take heavy toll of both the adults and the newly metamorphosed young at the breeding ponds. Reproductive success of the ant-eating frogs was much greater in 1954 when these ranids were unusually scarce. The short-tailed shrew is an important enemy. On occasion it took heavy toll of frogs trapped in pitfalls, and many of the larger adults were scarred or mutilated from bites, probably of the shrew.

Each of several frogs was found consistently under the same rock for periods of weeks. The hundreds of other frogs that were marked were rarely found twice in any one spot. Usually an individual recaptured after weeks or months was still near the original site. In many instances the distance involved was only a few yards, but there is some evidence that home ranges may be as long as 400 feet in greatest diameter. Of those caught in two or more different years only 15 per cent were shown to have moved more than 400 feet. These few exceptionally long movements, up to 2000 feet, involve shifts in home range or migrations motivated by reproductive urge.

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Check-list of the Birds of Kansas

BY

HARRISON B. TORDOFF

UNIVERSITY OF KANSAS
LAWRENCE
1956

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  6. Two new subspecies of Thomomys bottae from New Mexico and Colorado. By Keith R. Kelson. Pp. 59-71, 1 figure in text. October 1, 1951.
  7. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.
  8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.
  9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.
  *10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202. 68 figures in text. December 15, 1951.
  11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.
  12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.
  13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.

(Continued on inside of back cover)

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CHECK-LIST OF THE BIRDS OF KANSAS

By

Harrison B. Tordoff

Kansas was one of the first states for which a detailed book on birds was published (N. S. Goss, "History of the Birds of Kansas," Topeka, Kansas, 1891). Ornithological progress in Kansas in recent years, however, has not kept pace with work in many other states. As a result, knowledge of the birds of Kansas today is not sufficiently detailed to make possible a modern, definitive report. One purpose of this check-list is to show gaps in our information on birds of the state. Each student of birds can contribute importantly by keeping accurate records of nesting, distribution, and migration of any species in Kansas and by making these records available through publication in appropriate journals. The Museum of Natural History at the University of Kansas solicits records and specimens which contribute to our knowledge of birds in Kansas. Files and collections at the Museum are available to any qualified person for study.

The last state-wide list of birds was prepared by W. S. Long (Trans. Kansas Acad. Sci., 43, 1940:433-456). This list and the unpublished thesis from which the list was abstracted have been of great value in preparing the present report. Many other persons have contributed and among these the names of the following must be mentioned because of the value of their contributions: Ivan L. Boyd, L. B. Carson, Arthur L. Goodrich, Jr., Richard Graber, Jean Graber, Harold C. Hedges, R. F. Miller, John M. Porter, and Marvin D. Schwilling.

Full standing in this check-list has been given only to species for which at least one specimen from Kansas has been examined by some qualified student. Exceptions to this admittedly arbitrary rule have been made in three cases, Trumpeter Swan, Turkey, and Carolina Paroquet, because there is no reason to doubt that each of these three species once occurred in Kansas and because opportunity for obtaining specimens from Kansas has been lost through disappearance of the species from the state. Other species reported from the state but not authenticated by specimens have been relegated to the Hypothetical List and their names and my remarks concerning these birds are enclosed in brackets. This procedure is intended to encourage collection of such species; it is not intended necessarily to indicate doubt of a record. In the case of a carefully identified but uncollected accidental, opportunity for obtaining a specimen may not exist again for a long period. This is unfortunate but emphasizes the need for judicious collecting.

A total of 375 species (or 459 species and subspecies), of which four are introduced, is included in this check-list. Additionally, 15 species are discussed in the Hypothetical List. An asterisk (*) preceding an account indicates positive evidence of breeding in Kansas of the species so marked. The total of species known to have bred at least once in the state is 173. Nomenclature in this list follows the American Ornithologists' Union "Check-List of North American Birds" (1931, 4th edition) and its supplements. Species on the Hypothetical List are included in their current taxonomic position in the main list.

Gavia immer (Brünnich). Common Loon. Uncommon transient throughout state.

No subspecies recognized.

Gavia stellata (Pontoppidan). Red-throated Loon. Rare transient. One specimen: female (Univ. Michigan Mus. Zool. 65778), Marais des Cygnes River, near Ottawa, Franklin County, October 20, 1925, Captain Joe R. White. Several sight records from Shawnee and Johnson counties within past 10 years.

No subspecies recognized.

Colymbus grisegena. Red-necked Grebe. Rare transient. One specimen: female (KU 7697), Kansas River east of Lawrence, Douglas County, October 29, 1910, Logan I. Evans.

Subspecies in Kansas: *C. g. holböllii* (Reinhardt).

Colymbus auritus. Horned Grebe. Rare transient. Two authentic specimens: Manhattan, Riley County, September 30, 1878; male (KU 27465), 2½ miles north of Lawrence, Douglas County, November 16, 1945, E. C. Olson and Ralph L. Montell. Several sight records, from eastern, central, and western Kansas.

Subspecies in Kansas: *C. a. cornutus* Gmelin.

Colymbus caspicus. Eared Grebe. Regular transient throughout state; more common than Horned Grebe.

Subspecies in Kansas: *C. c. californicus* (Heermann).

Aechmophorus occidentalis (Lawrence). Western Grebe. Rare transient, perhaps more common in west but status poorly known.

No subspecies recognized.

* *Podilymbus podiceps.* Pied-billed Grebe. Common transient and irregular summer resident, rare winter resident.

Subspecies in Kansas: *P. p. podiceps* (Linnaeus).

Pelecanus erythrorhynchos Gmelin. White Pelican. Common transient throughout state. Occasional individuals, probably sick or wounded, remain beyond normal migration periods in spring and fall.

No subspecies recognized.

Pelecanus occidentalis. Brown Pelican. Accidental. One specimen: adult, sex not determined (KU 10468), Parker, Linn County, June, 1916, found dead by G. G. McConnell. One seen at Wichita, Sedgwick County, by R. H. Sullivan, April 25, 1910.

Subspecies in Kansas: *P. o. carolinensis* Gmelin.

* *Phalacrocorax auritus.* Double-crested Cormorant. Regular transient, in small to moderate numbers. One nesting record: several nests, eggs, and small young seen, Cheyenne Bottoms, Barton County, August, 1951, Otto Tiemeier.

Subspecies in Kansas: *P. a. auritus* (Lesson).

Phalacrocorax olivaceus. Mexican Cormorant. Accidental. One record: specimen taken 4 miles south of Lawrence, Douglas County, April 2, 1872. Present location unknown but specimen identified by S. F. Baird and R. Ridgway.

Subspecies in Kansas: *P. o. mexicanus* (Brandt).

Anhinga anhinga. Water-turkey. Accidental. Several specimens and sight observations are on record but most are prior to 1900. Several records and one specimen at Cheyenne Bottoms, Barton County, since 1928 (Frank Robl). In recent years, some reported Water-turkeys have proved to be cormorants.

Subspecies in Kansas: *A. a. leucogaster* (Vieillot).

Fregata magnificens. Man-o'-war-bird. Accidental. One record: specimen (present location unknown) taken on the North Fork of the Solomon River, Osborne County, August 16, 1880, by Frank Lewis.

Subspecies in Kansas: *F. m. rothschildi* Mathews.

* *Ardea herodias.* Great Blue Heron. Common transient and summer resident nesting in widely scattered colonies.

Subspecies in Kansas: three reported, *A. h. herodias* Linnaeus in northeast, *A. h. wardi* Ridgway in southeast, and *A. h. treganzai* Court in west, but status of these poorly known because of lack of sufficient breeding specimens.

Casmerodius albus. American Egret. Regular postbreeding summer visitant; occasional spring and summer resident. No definite nesting record.

Subspecies in Kansas: *C. a. egretta* (Gmelin).

* *Leucophoyx thula.* Snowy Egret. Regular postbreeding summer visitant; rare and local summer resident; occasional in spring.

One nesting record: two nests found, summer, 1952, 6 miles north and 4½ miles west of Garden City, Finney County, Marvin D. Schwilling.

Subspecies in Kansas: *L. t. thula* (Molina).

Hydranassa tricolor. Louisiana Heron. Accidental. Two records: specimen taken at Lake Inman, McPherson County, August 9, 1934, by R. E. Mohler and Richard H. Schmidt; one seen, 1½ miles south of Iatan Marsh, Atchison County (near Iatan, Missouri), September 12, 1948, first reported by R. F. Miller and Mr. and Mrs. Ivan L. Boyd, seen by several other observers.

Subspecies in Kansas: *H. t. ruficollis* (Gosse).

* *Florida caerulea.* Little Blue Heron. Regular postbreeding summer visitant; rare and local summer resident; occasional in spring. Usually more common than Snowy Egret. One nesting record: one nest found, summer, 1952, 6 miles north and 4½ miles west of Garden City, Finney County, Marvin D. Schwilling.

Subspecies in Kansas: *F. c. caerulea* (Linnaeus).

* *Butorides virescens.* Green Heron. Common transient and summer resident.

Subspecies in Kansas: *B. v. virescens* (Linnaeus).

* *Nycticorax nycticorax.* Black-crowned Night Heron. Transient and summer resident, breeding in scattered colonies.

Subspecies in Kansas: *N. n. hoactli* (Gmelin).

* *Nyctanassa violacea.* Yellow-crowned Night Heron. Summer resident throughout state, rare in north; numbers perhaps augmented in late summer by postbreeding stragglers.

Subspecies in Kansas: *N. v. violacea* (Linnaeus).

* *Botaurus lentiginosus* (Rackett). American Bittern. Common transient; summer resident locally. Two definite nesting records: nest with 4 newly hatched young (male collected, KU 30468), ½ mile east and 2 miles south of Welda, Anderson County, June 9, 1951, Maurice F. Baker; nest with eggs, 6 miles north and 3½ miles west of Kalvesta, Finney County, summer, 1952, Raymond Erkic (*fide* Marvin D. Schwilling).

No subspecies recognized.

* *Ixobrychus exilis.* Least Bittern. Transient and irregular summer resident. Two nests found at Lake Quivira, Johnson County, June 3, 1949, Harold C. Hedges; on June 28, one of the nests contained 4 eggs, on July 10 this nest was empty. No other definite nesting records.

Subspecies in Kansas: *I. e. exilis* (Gmelin).

Mycteria americana Linnaeus. Wood Ibis. Accidental. Several sight records and one specimen: male (KU 9489), 5 miles northeast of Goodland, Sherman County, October 4, 1913, Willis Feaster.

No subspecies recognized.

* *Plegadis mexicana* (Gmelin). White-faced Glossy Ibis. Irregular transient and summer visitant; more common in west. One definite nesting record: photograph of downy young ("Kansas Fish and Game," vol. 9, no. 3, Jan. 1952, p. 7) taken at Cheyenne Bottoms, Barton County, presumably in summer of 1951, by L. O. Nossaman. Frank Robl has seen individuals in summer in Cheyenne Bottoms on many occasions. Reports of Eastern Glossy Ibis (*Plegadis falcinellus*) in Kansas probably are based on dark-faced immatures of the present species, although the eastern species has been taken in Oklahoma.

No subspecies recognized.

Ajaia ajaja (Linnaeus). Roseate Spoonbill. Accidental. One authentic specimen (present location not known): male, near Douglass, on Four-Mile Creek, Butler County, March 20, 1899, taken by Dr. R. Matthews, identification verified by Jerold Volk and Wilfred Goodman.

No subspecies recognized.

Phoenicopterus ruber Linnaeus. Flamingo. Accidental. Two birds seen in autumn, 1928, at Little Salt Marsh, Stafford County, one of which was killed on opening day of duck season and now (1955) is mounted at Kansas Forestry, Fish, and Game Commission headquarters at Pratt.

No subspecies recognized.

Olor columbianus (Ord). Whistling Swan. Transient and winter resident, formerly common, now rare. Many specimens are on record; at least four were taken in winter.

No subspecies recognized.

Olor buccinator (Richardson). Trumpeter Swan. Formerly occasional migrant, no longer occurs in Kansas. All specimens from Kansas alleged to be of this species are actually Whistling Swans. The early sight records seem valid, however, and the species should remain on the state list.

No subspecies recognized.

**Branta canadensis*. Canada Goose. Common transient; some winter in suitable places. This species was found nesting along the Missouri River near Atchison by early explorers. Modern breeding records probably pertain to captives or their descendants.

Subspecies in Kansas: *B. c. moffitti* Aldrich, *B. c. leucopareia* (Brandt), *B. c. minima* Ridgway, and *B. c. hutchinsi* (Richardson) have been collected in

Kansas. Additionally, subspecies *interior* Todd and *parvipes* (Cassin) probably pass through the state but no specimens have been saved. Canada Geese of widely varying size are regularly seen in migration.

Branta bernicla. Brant. Accidental. Several sight records and one specimen: unsexed bird (KU 7490), Leavenworth County, November 15, 1879, A. Lange. Some hunters refer to immature Blue Geese as "brant." Orville O. Rice saw 4 brant 2 miles north of Burlington, near the Neosho River, Coffey County, March 24, 1955, that appeared to be Black Brant, *Branta nigricans* (Lawrence).

Subspecies in Kansas: *B. b. hrota* (Müller).

Anser albifrons. White-fronted Goose. Regular transient throughout state, more common in central and western parts.

Subspecies in Kansas: *A. a. frontalis* Baird.

Chen hyperborea. Snow Goose. Common transient throughout state.

Subspecies in Kansas: *C. h. hyperborea* (Pallas).

Chen caerulescens (Linnaeus). Blue Goose. Common transient in east, less common in central and western parts of state. In east, this species predominates in early spring migration whereas the Snow Goose is most numerous later. Hybrids between the two are regularly seen.

No subspecies recognized.

[*Chen rossii* (Cassin). Ross Goose. One reported at Wyandotte County Lake, November 22, 1951, by John Bishop. Placed in Hypothetical List in absence of a specimen.]

Dendrocygna bicolor. Fulvous Tree-duck. Accidental. Frank Robl carefully examined and identified three specimens killed in 1929 or 1930, in Cheyenne Bottoms, Barton County. None saved. Specimens collected also in nearby areas of Missouri.

Subspecies in Kansas: *D. b. helva* Wetmore and Peters, on geographical grounds.

* *Anas platyrhynchos.* Mallard. Abundant transient, regular winter resident, irregular and local summer resident. Modern breeding distribution poorly known but several nests found in widely scattered areas in past years. Nests regularly in Kearny, Finney, and Barton counties.

Subspecies in Kansas: *A. p. platyrhynchos* Linnaeus.

Anas rubripes Brewster. Black Duck. Regular but rare or uncommon transient and winter resident in east and central (Cheyenne Bottoms, Barton County) sections.

No subspecies recognized.

Anas fulvigula. Mottled Duck. Accidental. Four specimens allegedly of this species have been reported. Of these, two are actually Mallards, one is a Gadwall, and one, female, Neosho Falls, Woodson County, March 11, 1876, Goss, is a Mottled Duck.

Subspecies in Kansas: *A. f. maculosa* Sennett.

Anas strepera Linnaeus. Gadwall. Transient and occasional winter resident throughout state. Rare summer resident but no satisfactory nesting record reported.

No subspecies recognized.

* *Anas acuta* Linnaeus. Pintail. Abundant transient throughout state, irregular winter resident, local summer resident nesting in recent years in Barton, Finney, Meade, and Leavenworth counties, but summer distribution poorly known.

No subspecies recognized.

Anas carolinensis Gmelin. Green-winged Teal. Common transient, rare winter resident (records from Meade County and Kansas City).

No subspecies recognized.

* *Anas discors* Linnaeus. Blue-winged Teal. Common transient, locally common summer resident.

No subspecies recognized.

Anas cyanoptera. Cinnamon Teal. Rare transient in east, uncommon or fairly common transient in west.

Subspecies in Kansas: *A. c. septentrionalis* Snyder and Lumsden.

* *Spatula clypeata* (Linnaeus). Shoveller. Common transient throughout state. Frank Robl found a female with young in Cheyenne Bottoms, Barton County, in approximately 1930. Nest with eggs found 1½ miles south of Friend, Finney County, in spring, 1952, Marvin D. Schwilling.

No subspecies recognized.

[*Mareca penelope* (Linnaeus). European Widgeon. Carl and David Holmes reported a pair at Lake Shawnee, Shawnee County, April 16, 1954. Placed on Hypothetical List until a specimen is taken.]

Mareca americana (Gmelin). Baldpate. Common transient throughout state, rare winter resident.

No subspecies recognized.

* *Aix sponsa* (Linnaeus). Wood Duck. Transient, rare in west to locally common in extreme east. Summer resident in eastern part of state; breeding distribution poorly known.

No subspecies recognized.

* *Aythya americana* (Eyton). Redhead. Fairly common tran-

sient and occasional winter resident throughout state. Frank Robl found a nesting pair in Cheyenne Bottoms, Barton County, in 1928 (approximate). The adults were neither captives nor cripples.

No subspecies recognized.

Aythya collaris (Donovan). Ring-necked Duck. Fairly common transient throughout state, rare winter resident.

No subspecies recognized.

Aythya valisineria (Wilson). Canvas-back. Fairly common transient and occasional winter resident throughout state.

No subspecies recognized.

Aythya marila. Greater Scaup Duck. Rare transient, status poorly known. Several sight records, one in winter. Floyd T. Amsden, a competent sportsman and amateur ornithologist of Wichita, identified 3 male specimens killed 3 miles north and 1 mile east of Sharon, Barber County, on October 27 (2) and November 3 (1), 1951. Frank Robl has seen specimens killed in Cheyenne Bottoms, Barton County. Every effort should be made to preserve specimens from Kansas.

Subspecies in Kansas: *A. m. nearctica* Stejneger, on geographical grounds.

Aythya affinis (Eyton). Lesser Scaup Duck. Common transient throughout state. A few records of wintering and summering (nonbreeding) individuals.

No subspecies recognized.

Bucephala clangula. Golden-eye. Uncommon transient and winter resident. Specimens from Kansas alleged to be the Barrow Golden-eye (*Bucephala islandica*) all are of the present species.

Subspecies in Kansas: *B. c. americana* (Bonaparte).

Bucephala albeola (Linnaeus). Buffle-head. Fairly common transient and occasional winter resident throughout state.

No subspecies recognized.

Clangula hyemalis (Linnaeus). Old-squaw. Rare transient and winter visitant. At least five specimens taken (but only two or three preserved) and numerous sight records, from widely separated parts of state.

No subspecies recognized.

Somateria mollissima. Eider. Accidental. One record: immature male (KU 3620), Kansas River near Lecompton, Douglas County, November 3, 1891, A. L. Wiedman.

Subspecies in Kansas: *S. m. v. nigra* Bonaparte (identification checked by A. Wetmore).

Somateria spectabilis (Linnaeus). King Eider. Accidental. One record: immature male (KU 27487), Kansas River 1 mile east of Lawrence, Douglas County, November 27, 1947, R. L. Montell.

No subspecies recognized.

Melanitta deglandi. White-winged Scoter. Rare transient. Nine specimens from Douglas and Leavenworth counties, taken from 1927 to 1938; several sight records from eastern Kansas.

Subspecies in Kansas: *M. d. deglandi* (Bonaparte).

Melanitta perspicillata (Linnaeus). Surf Scoter. Rare transient. Eight known specimens (three of which are now in University of Kansas collection), all taken in autumn, seven in Douglas County, one in Sedgwick County; several sight records from eastern Kansas.

No subspecies recognized.

Oidemia nigra. Common Scoter. Accidental. The two preserved specimens from Kansas supposedly of this species are actually Surf Scoters. L. B. Carson, however, identified an adult male Common Scoter killed by a hunter at Horton Lake, Brown County, in the early 1930's. Others have been seen by reliable field observers. Every effort should be made to secure specimens from Kansas.

Subspecies in Kansas: *O. n. americana* Swainson, on geographical grounds.

* *Oxyura jamaicensis.* Ruddy Duck. Common transient throughout state, rare winter resident. One breeding record: Frank Robl saw an adult female with one small young at Cheyenne Bottoms, Barton County, in approximately 1929.

Subspecies in Kansas: *O. j. rubida* (Wilson).

Lophodytes cucullatus (Linnaeus). Hooded Merganser. Uncommon transient and winter resident throughout state. Probably nests occasionally (two specimens at KU taken in east in June), but no proof of this available.

No subspecies recognized.

Mergus merganser. American Merganser. Common transient and winter resident throughout state.

Subspecies in Kansas: *M. m. americanus* Cassin.

Mergus serrator. Red-breasted Merganser. Uncommon transient throughout state; probably also rare winter resident but records lacking. This species is more common than Hooded Merganser in west, less common than Hooded in east.

Subspecies in Kansas: *M. s. serrator* Linnaeus.

* *Cathartes aura.* Turkey Vulture. Common transient throughout state; common summer resident west at least to Clark County. Breeding distribution in west poorly known.

Subspecies in Kansas: *C. a. teter* Friedmann.

* *Coragyps atratus* (Meyer). Black Vulture. Once occurred in southeast, but no record since 1885. Goss quotes Dr. George Lisle ("a close observer") as finding this species common and breeding at Chetopa, Labette County, on the Oklahoma line, prior to 1883. Lisle found a nest with two eggs in 1858. Goss also reports one killed by Watson at Ellis, Ellis County, on March 27, 1885, but the location of the specimen is unknown. The species may still occur in southeastern Kansas.

No subspecies recognized.

* *Elanoïdes forficatus.* Swallow-tailed Kite. Formerly summer resident in at least eastern half of state. Last specimen from Kansas taken by Dr. G. C. Rinker at Hamilton, Greenwood County, May 17, 1914.

Subspecies in Kansas: *E. f. forficatus* (Linnaeus).

* *Ictinia misisippiensis* (Wilson). Mississippi Kite. Common summer resident in south-central Kansas, east to Harvey, north to Barton, and west to Kearny counties. Occasional records from Douglas (nested once), Johnson, Greenwood, and Hamilton counties.

No subspecies recognized.

Accipiter gentilis. Goshawk. Rare and irregular winter visitor in east. Status in west unknown.

Subspecies in Kansas: *A. g. atricapillus* (Wilson).

* *Accipiter striatus.* Sharp-shinned Hawk. Transient and winter resident throughout state; less common in east. Status in summer poorly known; one nest found in Cloud County, July 11, 1938, J. M. Porter.

Subspecies in Kansas: *A. s. velox* (Wilson).

* *Accipiter cooperii* (Bonaparte). Cooper Hawk. Resident throughout state but nesting records only from the eastern half, west to Cloud County.

No subspecies recognized.

* *Buteo jamaicensis.* Red-tailed Hawk. Abundant transient and winter resident in east; in High Plains of west, largely restricted to river bottoms in winter. Common summer resident in east; status in summer in west poorly known.

Subspecies in Kansas: *B. j. borealis* (Gmelin) is the breeding bird of eastern Kansas. *B. j. calurus* Cassin probably nests in west but no specimens available. *B. j. borealis, B. j. calurus, B. j. kriderii* Hoopes, and *B. j. harlani* (Audubon), the latter considered here as conspecific with *jamaicensis,* all occur as transients and winter residents. More specimens needed to establish details of distribution of various subspecies.

* *Buteo lineatus.* Red-shouldered Hawk. Uncommon transient and summer resident and irregular winter resident in eastern Kansas.

Breeding records from Leavenworth and Woodson counties; doubtless breeds in other eastern counties but definite evidence lacking.

Subspecies in Kansas: *B. l. lineatus* (Gmelin).

* *Buteo platypterus.* Broad-winged Hawk. Fairly common transient and local summer resident in eastern Kansas. Breeding records only from Douglas, Leavenworth, and Johnson counties, where species nests regularly.

Subspecies in Kansas: *B. p. platypterus* (Vieillot).

* *Buteo swainsoni* Bonaparte. Swainson Hawk. Abundant transient in west, fairly common in east. Nests commonly throughout western two-thirds of state and at least occasionally in eastern portion. Supposed winter records should be substantiated by specimens.

No subspecies recognized.

Buteo lagopus. Rough-legged Hawk. Winter resident, fairly common in east to common in west.

Subspecies in Kansas: *B. l. s. johannis* (Gmelin).

* *Buteo regalis* (Gray). Ferruginous Rough-leg. Common transient and winter resident in west, rare in east. Rare summer resident in west. Two nesting records: nest with four young, south fork of Smoky Hill River, near Wallace, May 27, 1883, Goss; nest with three young, west of Russell Springs, Logan County, May 29, 1954, Marvin D. Schwilling.

No subspecies recognized.

Parabuteo unicinctus. Harris Hawk. Accidental. Two records: male, Wichita, Sedgwick County, December 14, 1918, LeRoy Snyder; female (KU 10752), 7½ miles southwest of Lawrence, Douglas County, December 25, 1918, Fred Hastie.

Subspecies in Kansas: *P. u. harrisi* (Audubon).

* *Aquila chrysaëtos.* Golden Eagle. Formerly common resident throughout state. Now common in winter in west to rare in east. One positive nesting record: a pair nested for several years (prior to 1891) in southeastern Comanche County on a high gypsum ledge, Goss.

Subspecies in Kansas: *A. c. canadensis* (Linnaeus).

Haliaeetus leucocephalus. Bald Eagle. Rare transient and winter resident in east; fairly common winter resident in west, where large numbers may gather to roost.

Subspecies in Kansas: *H. l. alascanus* Townsend. Previous students refer all Bald Eagles from the state to *H. l. leucocephalus* (Linnaeus) but specimens in the K. U. collection, all taken in winter, are large (three females, wing, 645, 655, 680 mm.) and are clearly of the northern subspecies.

* *Circus cyaneus.* Marsh Hawk. Resident, common in winter, less common and local in summer.

Subspecies in Kansas: *C. c. hudsonius* (Linnaeus).

Pandion haliaetus. Osprey. Occurs irregularly throughout state but less frequently in west. Most records in spring and autumn but a few at other seasons. No definite nesting record.

Subspecies in Kansas: *P. h. carolinensis* (Gmelin).

Falco rusticolus. Gyrfalcon. Accidental. One specimen: Manhattan, Riley County, December 1, 1880, A. L. Runyan (specimen at Kansas State College).

Subspecies in Kansas: *F. r. obsoletus* Gmelin.

Falco mexicanus Schlegel. Prairie Falcon. Rare summer and fairly common winter resident in west; occasional transient and winter resident in east. No satisfactory breeding records.

No subspecies recognized.

* *Falco peregrinus.* Duck Hawk. Rare transient and winter resident, probably more common in west. Formerly nested but no nesting record since before 1900.

Subspecies in Kansas: *F. p. anatum* Bonaparte.

Falco columbarius. Pigeon Hawk. Uncommon transient and rare winter resident in east; more common in migration in west but status there in winter not known.

Subspecies in Kansas: *F. c. columbarius* Linnaeus is most frequent in eastern part, west to Reno County; *F. c. richardsonii* Ridgway is the common subspecies in west, occasional in east; *F. c. bendirei* Swann is known in Kansas from one specimen (KU 4425) from Ellis County, October, 1875, taken by Dr. L. Watson (identified by James L. Peters).

* *Falco sparverius.* Sparrow Hawk. Common resident and transient throughout state (but status in winter in northwest not known).

Subspecies in Kansas: *F. s. sparverius* Linnaeus.

Bonasa umbellus. Ruffed Grouse. Formerly common resident in eastern part; now probably extirpated in state but observers in extreme east should watch for it. One authentic specimen (KU 31944), southeastern Kansas, between 1885 and 1910, Alexander J. C. Roese. No definite nesting record.

Subspecies in Kansas: *B. u. umbellus* (Linnaeus).

* *Tympanuchus cupido.* Greater Prairie Chicken. Resident, but highly local; absent in southwestern quarter of state.

Subspecies in Kansas: *T. c. pinnatus* (Brewster).

* *Tympanuchus pallidicinctus* (Ridgway). Lesser Prairie Chicken. Resident, but local, in southwestern quarter of state, north to Hamilton and Finney counties and east to Pawnee and

Barber counties. A few old records east to Anderson and Neosho counties in winter.

No subspecies recognized.

Pedioecetes phasianellus. Sharp-tailed Grouse. Formerly resident in western part of state; scattered old records from eastern localities. Now extirpated, or nearly so, in Kansas; observers in northwestern counties should watch for it. No definite nesting record.

Subspecies in Kansas: *P. p. jamesi* Lincoln.

* *Colinus virginianus.* Bob-white. Resident, common in east, less common and local in west.

Subspecies in Kansas: *C. v. virginianus* (Linnaeus) in east, intergrading through central part with *C. v. taylori* Lincoln in west.

* *Callipepla squamata.* Scaled Quail. Locally common resident in southwest, formerly north to Wallace County but now primarily south of Arkansas River, eastern limit not known. Breeding records from Hamilton, Kearny, Finney, Stanton, Morton, Stevens, and Clark counties, Marvin D. Schwilling.

Subspecies in Kansas: *C. s. pallida* Brewster.

* *Phasianus colchicus* Linnaeus. Ring-necked Pheasant. Introduced. Common in western two-thirds, gradually invading east where a few are now found in most counties.

Origin of North American stock obscure; no subspecies now recognized here.

Meleagris gallopavo. Turkey. Formerly common resident, west along streams at least to Riley County; now extirpated in Kansas. No known specimen from Kansas with authentic data. No definite nesting record.

Subspecies in Kansas: *M. g. silvestris* Vieillot.

Grus americana (Linnaeus). Whooping Crane. Regular transient, now rare. Probably most individuals go through east-central part of state. Several early specimens from state and several recent sight records and one specimen: adult female (KU 31198), found crippled 8½ miles south of Sharon, Barber County, October 31, 1952, Thane S. Robinson.

No subspecies recognized.

Grus canadensis. Sandhill Crane. Transient, rare in east, common to abundant in west.

Subspecies in Kansas: *G. c. canadensis* (Linnaeus) and *G. c. tabida* (Peters); comparative status of the two subspecies not known.

* *Rallus elegans.* King Rail. Transient and summer resident, locally common.

Subspecies in Kansas: *R. e. elegans* Audubon.

* *Rallus limicola.* Virginia Rail. Transient and summer resident, but breeding status poorly known. One breeding record: adult with six small, downy young, 8 miles south of Richfield, Morton County, May 24, 1950, Richard and Jean Graber.

Subspecies in Kansas: *R. l. limicola* Vieillot.

* *Porzana carolina* (Linnaeus). Sora. Common transient throughout state; status in summer poorly known. Two breeding records: Osawatomie, Miami County, prior to 1914 (no other details), record by Colvin, a careful observer; two nests, at least one with eggs, Finney County State Lake, August 21, 1951, Marvin D. Schwilling. Additional nesting records should be sought.

No subspecies recognized.

Coturnicops noveboracensis. Yellow Rail. Rare or generally overlooked transient. Records only from eastern part of state (west to Sedgwick County).

Subspecies in Kansas: *C. m. noveboracensis* (Gmelin).

* *Laterallus jamaicensis.* Black Rail. Rare or generally overlooked summer resident. At least ten records, including at least seven specimens from widely scattered localities. Two breeding records: nest with eight eggs, Manhattan, Riley County, June, 1880, C. P. Blachly; nest with nine eggs, near Garden City, Finney County, June 6, 1889, H. W. Menke.

Subspecies in Kansas: *L. j. jamaicensis* (Gmelin).

Porphyrula martinica (Linnaeus). Purple Gallinule. Rare and irregular summer visitant. Five specimens taken in April and June in Douglas, Sedgwick, and Riley counties. Several sight records from eastern Kansas.

No subspecies recognized.

* *Gallinula chloropus.* Florida Gallinule. Rare summer resident; status poorly known. Two breeding records: nest found "on a board," Coffey County, June (year not given), P. B. Peabody; nest (female, KU 27509, and two eggs taken), 3 miles northeast of Lawrence, Douglas County, May 22, 1945 (previously published as 1946), R. L. Montell.

Subspecies in Kansas: *G. c. cachinnans* Bangs.

* *Fulica americana.* American Coot. Uncommon summer resident, abundant transient, and local winter resident in east and central parts; status in west poorly known. Breeding record: 3 newly hatched young (KU 16694-6), Little Salt Marsh, Stafford County, June 13, 1927, H. C. Parker and W. H. Burt. The few other nesting localities include one in Finney County.

Subspecies in Kansas: *F. a. americana* Gmelin.

Charadrius hiaticula. Semipalmated Plover. Regular transient throughout state, often fairly common.

Subspecies in Kansas: *C. h. semipalmatus* Bonaparte.

Charadrius melodus. Piping Plover. Rare transient. Three specimens from Douglas County, March and April, and a female (KU 15492) from Little Salt Marsh, Stafford County, July 16, 1925, T. E. White. Nests in Nebraska, south at least to Lincoln; observers in north-central Kansas should watch for possible breeding birds.

Subspecies in Kansas: *C. m. circumcinctus* (Ridgway).

* *Charadrius alexandrinus.* Snowy Plover. Summer resident on salt plains of Clark, Comanche, Stafford, Barton, and probably other counties. Breeding range in Kansas poorly known. One definite nesting record: adults with young, and one nest with 3 eggs, Comanche County, June 18, 1886, Goss. One female (KU 7787), from Lawrence, Douglas County, April 22, 1909, L. L. Dyche.

Subspecies in Kansas: *C. a. tenuirostris* (Lawrence).

* *Charadrius vociferus.* Killdeer. Common transient and summer resident throughout state. Occasional winter resident.

Subspecies in Kansas: *C. v. vociferus* Linnaeus.

* *Eupoda montana* (Townsend). Mountain Plover. Summer resident in High Plains of western Kansas, but current status poorly known. Many specimens from west and one positive breeding record: two half-grown, partly downy males (KU 5512, 5513), 5 miles south of Tribune, Greeley County, June 21, 1911, Bunker and Rocklund.

No subspecies recognized.

Pluvialis dominica. Golden Plover. Regular transient in east, sometimes common; more common in spring than in autumn. Formerly abundant; status in west not known.

Subspecies in Kansas: *P. d. dominica* (Müller).

Squatarola squatarola (Linnaeus). Black-bellied Plover. Regular transient throughout state.

No subspecies recognized.

Arenaria interpres. Ruddy Turnstone. Rare transient. Several sight records from eastern part of state and two specimens: one killed at Topeka, Shawnee County, August 16, 1898, F. W. Forbes (location of specimen unknown); male, Hamilton, Greenwood County, October 1, 1911, G. C. Rinker.

Subspecies in Kansas: *A. i. morinella* (Linnaeus).

* *Philohela minor* (Gmelin). American Woodcock. Uncommon transient west to Scott and Kearny counties. Probably does not occur farther west. One early nesting record: adult with several

"at least one-fourth grown" young, near Neosho Falls, Woodson County, May 25, 1874, Goss.

No subspecies recognized.

Capella gallinago. Wilson Snipe. Common transient and occasional winter resident throughout state.

Subspecies in Kansas: *C. g. delicata* (Ord).

* *Numenius americanus.* Long-billed Curlew. Transient and uncommon summer resident in west; occasional transient in east. Female and two downy young (KU 11607, 8, 9) taken 1 mile from Spring Creek, Morton County, June 27, 1927, W. H. Burt and L. V. Compton.

Subspecies in Kansas: *N. a. americanus* Bechstein is the breeding form; *N. a. parvus* Bishop occurs in migration (specimens from Riley, Lyon, and Douglas counties).

[*Numenius phaeopus.* Hudsonian Curlew. Reported by Goss, and one seen at Iatan Marsh, Atchison County, May 16, 1948, by Harold C. Hedges, but here placed in Hypothetical List until a specimen from Kansas is taken.]

Numenius borealis (Forster). Eskimo Curlew. Formerly abundant transient in eastern Kansas; now extinct, or nearly so. One unsexed bird (KU 6951) taken in Douglas County, May 6, 1873, by N. J. Stevens.

No subspecies recognized.

* *Bartramia longicauda* (Bechstein). Upland Plover. Abundant transient and locally common summer resident in suitable habitat; most numerous in west. Nesting records from Johnson, Wabaunsee, Chase, Finney, and Kearny counties.

No subspecies recognized.

* *Actitis macularia* (Linnaeus). Spotted Sandpiper. Common transient and summer resident throughout state. Breeding records from Leavenworth County and Kansas City region.

No subspecies recognized.

Tringa solitaria. Solitary Sandpiper. Common transient throughout state.

Subspecies in Kansas: *T. s. solitaria* Wilson is most common in eastern part and *T. s. cinnamomea* (Brewster) is most common in western part of Kansas, with much overlap of the two.

Catoptrophorus semipalmatus. Willet. Transient throughout state, usually uncommon, but sometimes locally common.

Subspecies in Kansas: *C. s. inornatus* (Brewster). *C. s. semipalmatus* (Gmelin) has been reported, probably erroneously; all specimens seen are of the western subspecies, *inornatus*.

Totanus melanoleucus (Gmelin). Greater Yellow-legs. Common transient throughout state.

No subspecies recognized.

Totanus flavipes (Gmelin). Lesser Yellow-legs. Common transient throughout state.

No subspecies recognized.

Calidris canutus. American Knot. Rare transient. Sight records from eastern and western Kansas; only one specimen preserved, Hamilton, Greenwood County, September 19, 1911, G. C. Rinker.

Subspecies in Kansas: *C. c. rufa* (Wilson).

Erolia melanotos (Vieillot). Pectoral Sandpiper. Common transient through state.

No subspecies recognized.

Erolia fuscicollis (Vieillot). White-rumped Sandpiper. Common transient throughout state.

No subspecies recognized.

Erolia bairdii (Coues). Baird Sandpiper. Common transient in east; abundant transient in west.

No subspecies recognized.

Erolia minutilla (Vieillot). Least Sandpiper. Common transient throughout state, but less numerous in west than in east.

No subspecies recognized.

Erolia alpina. Red-backed Sandpiper. Rare or uncommon transient; reported only from eastern half of state, west to Cloud County. Few specimens have been preserved.

Subspecies in Kansas: *E. a. pacifica* (Coues).

Limnodromus griseus. Short-billed Dowitcher. Rare or uncommon transient in east, status in west not known. One specimen: male (KU 29403), 3 miles east of Lawrence, Douglas County, May 14, 1946, R. L. Montell. Dowitchers having noticeably short bills should be collected when possible.

Subspecies in Kansas: *L. g. hendersoni* Rowan.

Limnodromus scolopaceus (Say). Long-billed Dowitcher. Common transient throughout state.

No subspecies recognized.

Micropalama himantopus (Bonaparte). Stilt Sandpiper. Common transient throughout state.

No subspecies recognized.

Ereunetes pusillus (Linnaeus). Semipalmated Sandpiper. Common transient throughout state.

No subspecies recognized.

Ereunctes mauri Cabanis. Western Sandpiper. Uncommon transient in east; probably common in west but status there unknown.

No subspecies recognized.

Tryngites subruficollis (Vieillot). Buff-breasted Sandpiper. Uncommon but regular transient in autumn in eastern Kansas, west to Republic County; few spring records.

No subspecies recognized.

Limosa fedoa (Linnaeus). Marbled Godwit. Rare or uncommon transient throughout state. Status somewhat uncertain because some observers confuse this species with female Hudsonian Godwits. The latter are larger and often much duller than male Hudsonian Godwits. Marbled Godwits, however, show no contrasting tail pattern in flight.

No subspecies recognized.

Limosa haemastica (Linnaeus). Hudsonian Godwit. Uncommon transient in eastern and central Kansas; status in west poorly known (reported from Ness and Kearny counties).

No subspecies recognized.

Crocethia alba (Pallas). Sanderling. Rare transient in eastern and central Kansas; status in west not known. Three specimens have been taken, two from Douglas County (October) and one from Stafford County (July).

No subspecies recognized.

* *Recurvirostra americana* Gmelin. Avocet. Uncommon transient in east; common transient and uncommon summer resident in west. Breeding records from Kearny, Finney, Haskell, Meade, and Barton counties.

No subspecies recognized.

Himantopus mexicanus (Müller). Black-necked Stilt. Rare transient. Records from Crawford, Sedgwick, Cloud, Stafford, Finney, and Kearny counties; few recent records. No satisfactory nesting record.

No subspecies recognized.

Phalaropus fulicarius (Linnaeus). Red Phalarope. Very rare transient. Two specimens: female (KU 3778), Lake View, Douglas County, November 5, 1905, E. E. Brown; male (Ottawa Univ. 96), near Ottawa, Franklin County, October 25, 1926, Wesley Clanton (identification checked by Tordoff).

No subspecies recognized.

* *Steganopus tricolor* Vieillot. Wilson Phalarope. Common transient throughout state. One definite nesting record: adult male with downy young, Cheyenne Bottoms, Barton County, June 26,

1954, Ted F. Andrews and Homer Stephens. Goss mentioned "breeding birds" in Meade County but the record is not convincing.

No subspecies recognized.

Lobipes lobatus (Linnaeus). Northern Phalarope. Rare transient. Goss shot five and preserved one (now in Goss collection) of 17 or 18 seen at Fort Wallace, Wallace County, May 25, 1883. Several sight records.

No subspecies recognized.

Stercorarius pomarinus (Temminck). Pomarine Jaeger. Accidental. One record: immature male (KU 6967), Kansas River near Lawrence, Douglas County, October 10, 1898, Gus Berger and Banks Brown. This specimen erroneously reported as a Parasitic Jaeger, *Stercorarius parasiticus* (Linnaeus), in previous lists of birds of Kansas.

No subspecies recognized.

Stercorarius longicaudus Vieillot. Long-tailed Jaeger. Accidental. One record: female (KU 32610), Cheyenne Bottoms, Barton County, June 23, 1955, William M. Lynn and Larry D. Mosby.

No subspecies recognized.

[*Larus hyperboreus*. Glaucous Gull. One bird with crippled leg seen at Lake Shawnee, Shawnee County, January 27, 1951, and several days thereafter, by many observers including the author. Placed on Hypothetical List until specimen is taken in Kansas.]

Larus argentatus. Herring Gull. Transient, regular along Missouri River, uncommon to rare elsewhere in state; probably rare winter resident.

Subspecies in Kansas: *L. a. smithsonianus* Coues.

Larus californicus Lawrence. California Gull. Accidental. One record: specimen (location unknown) taken by Goss, Arkansas River, Reno County, October 20, 1880.

No subspecies recognized.

Larus delawarensis Ord. Ring-billed Gull. Transient, locally common; rare winter resident.

No subspecies recognized.

Larus atricilla Linnaeus. Laughing Gull. Accidental. One specimen taken 3 miles east and 2½ miles south of Canton, in Marion County, May 15, 1933, Richard H. Schmidt (specimen in his collection); sight records from Barton and Shawnee counties.

No subspecies recognized.

Larus pipixcan Wagler. Franklin Gull. Transient, abundant in west, common in east.

No subspecies recognized.

Larus philadelphia (Ord). Bonaparte Gull. Rare transient. All specimens from eastern part, west to Cloud County; status in west not known.

No subspecies recognized.

[*Rissa tridactyla.* Kittiwake. Immature bird seen at Lake Shawnee, Shawnee County, October 20, 1951, by L. B. Carson and O. S. Pettingill, Jr. In the absence of a specimen, the species is placed on the Hypothical List.]

Xema sabini. Sabine Gull. Three records: immature male, taken at Humboldt, Allen County, September 19, 1876, Peter Long (now in Goss collection): immature male, taken at Hamilton, Greenwood County, October 3, 1909, G. C. Rinker; immature bird seen but not collected on October 18, 28, and 29, 1952, at Lake Shawnee, Shawnee County, by several observers (Orville O. Rice secured good photographs of this bird).

Subspecies in Kansas: *X. s. sabini* (Sabine).

Sterna forsteri Nuttall. Forster Tern. Transient, locally common in eastern half of state; status in west unknown.

No subspecies recognized.

Sterna hirundo. Common Tern. Rare transient. Two specimens: female, Anderson County, May 11, 1878 (in Goss collection); male, Munger's Lake, near Hamilton, Greenwood County, September 2, 1912, G. C. Rinker.

Subspecies in Kansas: *S. h. hirundo* Linnaeus.

* *Sterna albifrons.* Least Tern. Uncommon transient and local summer resident throughout state. One definite nesting record: five nests, each with two eggs, Arkansas River at Coolidge, Hamilton County, July 1, 1936, Otto Tiemeier.

Subspecies in Kansas: *S. a. athalassos* Burleigh and Lowery.

Hydroprogne caspia (Pallas). Caspian Tern. Uncommon transient throughout state. Many sight records but only one specimen: female (KU 17147), Douglas County, September 27, 1928, Harold Standing (skin and body skeleton of this tern saved; erroneously reported previously as two specimens).

No subspecies recognized.

Chlidonias niger. Black Tern. Common transient and, in north-central part, regular summer resident but no positive breeding record.

Subspecies in Kansas: *C. n. surinamensis* (Gmelin).

* *Columba livia* Gmelin. Rock Dove. Introduced. Common around habitations; nesting locally in feral state on cliffs in western Kansas.

No subspecies recognized because of mixed ancestry of birds introduced into New World.

* *Zenaidura macroura.* Mourning Dove. Common transient and summer resident, uncommon winter resident.

Subspecies in Kansas: *Z. m. carolinensis* (Linnaeus) in east, *Z. m. marginella* (Woodhouse) in west, intergrading in central part.

* *Ectopistes migratorius* (Linnaeus). Passenger Pigeon. Extinct. Formerly irregular transient and summer resident. Two specimens, both males, taken at Neosho Falls, Woodson County, April 14, 1876, by Goss, who also reported this species to nest there occasionally.

No subspecies recognized.

[*Columbigallina passerina.* Ground Dove. One seen on Kansas River, 3 miles west of St. Marys, Pottawatomie County, November 11, 1954, by Thomas A. Hoffman and James Mulligan. Placed in Hypothetical List in absence of a specimen from Kansas.]

[*Scardafella inca* (Lesson). Inca Dove. One seen daily at Halstead, Harvey County, November 10, 1951, to January 21, 1952, by Edna L. Ruth and others. One seen in Topeka, Shawnee County, last week of June, 1952, E. J. Rice. Placed in Hypothetical List in absence of a specimen from Kansas.]

**Conuropsis carolinensis.* Carolina Paroquet. Extinct. Formerly common resident in wooded areas of east; west along stream bottoms. Goss reported nesting of small flock near Neosho Falls, Woodson County, in spring, 1858. No specimen from Kansas preserved.

Subspecies in Kansas: *C. c. ludovicianus* (Gmelin), on geographical grounds.

* *Coccyzus americanus.* Yellow-billed Cuckoo. Common transient and summer resident throughout state.

Subspecies in Kansas: *C. a. americanus* (Linnaeus).

* *Coccyzus erythropthalmus* (Wilson). Black-billed Cuckoo. Uncommon transient and summer resident. Nesting records: female (KU 15480) and nest containing two Black-billed Cuckoo eggs and one Yellow-billed Cuckoo egg, 7½ miles southwest of Lawrence, Douglas County, June 5, 1926, Charles D. Bunker; nests found in Cloud County in June, 1932 (1), 1933 (1), 1934 (1), 1935 (1), 1938 (2), J. M. Porter.

No subspecies recognized.

* *Geococcyx californianus* (Lesson). Road-runner. Resident in south-central and southwestern Kansas; abundance and distribution subject to wide fluctuation, current status unknown. Four nests found, April to July, 1934, 4½ miles east of Arkansas City, Cowley County, Walter Colvin.

No subspecies recognized.

Crotophaga sulcirostris. Groove-billed Ani. Accidental. Three records: specimen (KU 31948), McCune, Crawford County, between 1885 and 1910, Alexander J. C. Roese; specimen, Lyon County, November 1, 1904; male (KU 31951), 6¾ miles northeast of Blue Rapids, Marshall County, October 28, 1952, Elizabeth G. McCleod.

Subspecies in Kansas: *C. s. sulcirostris* Swainson.

* *Tyto alba.* Barn owl. Uncommon resident throughout state.

Subspecies in Kansas: *T. a. pratincola* (Bonaparte).

* *Otus asio.* Screech Owl. Common resident throughout state.

Subspecies in Kansas: Following reported: *O. a. naevius* (Gmelin) in northeast, *O. a. hasbroucki* Ridgway in south-central, *O. a. aikeni* (Brewster) and *O. a. swenki* Oberholser in west. The status of these subspecies is poorly known; additional breeding specimens and revisionary study are needed.

* *Bubo virginianus.* Horned Owl. Common resident throughout state.

Subspecies in Kansas: *B. v. virginianus* (Gmelin) in east, *B. v. occidentalis* Stone in west.

Nyctea scandiaca (Linnaeus). Snowy Owl. Rare and irregular winter visitant throughout state.

No subspecies recognized.

[*Surnia ulula.* Hawk Owl. None of the several sight records from Kansas is convincing to me. Reports from eastern Kansas indicating regular occurrence there of this far-northern species are surely erroneous and probably pertain to Short-eared Owls.]

* *Speotyto cunicularia.* Burrowing Owl. Common summer resident in west; irregular transient in east. Numbers seem to be decreasing.

Subspecies in Kansas: *S. c. hypugea* (Bonaparte).

* *Strix varia.* Barred Owl. Resident in east, locally fairly common. Status in west not known.

Subspecies in Kansas: *S. v. georgica* Latham in southeast; *S. v. varia* Barton elsewhere in state.

* *Asio otus.* Long-eared Owl. Uncommon summer resident, locally common transient and winter resident throughout state. Nesting records from Ottawa, Douglas, Doniphan, and Meade counties. Status in summer poorly known.

Subspecies in Kansas: *A. o. wilsonianus* (Lesson).

* *Asio flammeus.* Short-eared Owl. Resident, probably throughout state, in suitable habitat. More common in winter. Nesting records from Woodson, Republic, and Marshall counties.

Subspecies in Kansas: *A. f. flammeus* (Pontoppidan).

**Aegolius acadicus.* Saw-whet Owl. Rare winter resident throughout state. One nesting record: a pair found in Kansas City, Wyandotte County, in winter, 1950, remained at least to September, 1951, and were seen with young birds in summer, 1951, John Bishop.

Subspecies in Kansas: *A. a. acadicus* (Gmelin).

* *Caprimulgus carolinensis* Gmelin. Chuck-will's-widow. Locally common summer resident in eastern Kansas, western limit of distribution poorly known.

No subspecies recognized.

* *Caprimulgus vociferus.* Whip-poor-will. Locally common summer resident in eastern Kansas; two specimens reported from Finney County, but status in west poorly known. Two nests reported, at Geary, Doniphan County, June 16 and June 14 to July 3, 1923, by Linsdale. In recent years, Chuck-will's-widows seem to have increased at the expense of Whip-poor-wills in Kansas.

Subspecies in Kansas: *C. v. vociferus* Wilson.

* *Phalaenoptilus nuttallii.* Poor-will. Summer resident, common in west, rare and local in east.

Subspecies in Kansas: *P. n. nuttallii* (Audubon).

* *Chordeiles minor.* Nighthawk. Common transient and summer resident throughout state.

Subspecies in Kansas: Nesting; *C. m. minor* (Forster) in northeast, *C. m. chapmani* Coues in southeast, and *C. m. howelli* Oberholser in west, intergrading with one another through fairly broad zones. Migration; *C. m. sennetti* Coues throughout state.

* *Chaetura pelagica* (Linnaeus). Chimney Swift. Common transient and summer resident in east; status in west poorly known. Schwilling reports this species only in migration in Finney and neighboring counties.

No subspecies recognized.

* *Archilochus colubris* (Linnaeus). Ruby-throated Hummingbird. Common transient and summer resident in east; much less common in west, status there poorly known.

No subspecies recognized.

Stellula calliope (Gould). Calliope Hummingbird. One record: immature female, 8 miles south of Richfield and 6 miles east of Kansas Highway 27, Morton County, September 3, 1952, Jean W. Graber.

No subspecies recognized.

* *Megaceryle alcyon.* Belted Kingfisher. Common summer resident and uncommon winter resident throughout state.

Subspecies in Kansas: *M. a. alcyon* (Linnaeus).

* *Colaptes auratus.* Yellow-shafted Flicker. Common resident

throughout state, but partly replaced in west by Red-shafted Flicker and hybrids between the two species.

Subspecies in Kansas: *C. a. auratus* (Linnaeus) in southeast, *C. a. luteus* Bangs in remainder of state. *C. a. borealis* Ridgway has been reported in winter in east.

* *Colaptes cafer.* Red-shafted Flicker. Common resident in west, hybridizing with, and replaced by, Yellow-shafted Flicker eastward. Uncommon winter resident in east.

Subspecies in Kansas: *C. c. collaris* Vigors.

* *Dryocopus pileatus.* Pileated Woodpecker. Formerly common resident in eastern Kansas, now much reduced in numbers and distribution. Recent sight records from Leavenworth, Wyandotte, Douglas, Miami, Linn, and Neosho counties may indicate that this species is increasing in its former range. Definite nesting records only from Linn County where Frank Wood and Ivan Sutton found a nest with 4 eggs and a nest with two young and one egg, along Marais des Cygnes River, near Pleasanton, some years ago. Eunice and Wilson Dingus have noted this species at Mound City, Linn County, regularly for several years.

Subspecies in Kansas: *D. p. abieticola* (Bangs) in northeast, *D. p. pileatus* (Linnaeus) in southeast.

* *Centurus carolinus.* Red-bellied Woodpecker. Common resident in eastern part, breeding west at least to Comanche County; additional records in west from Morton, Finney, and Kearny counties.

Subspecies in Kansas: *C. c. zebra* (Boddaert).

* *Melanerpes erythrocephalus.* Red-headed Woodpecker. Common transient and summer resident throughout state. Occasional winter resident west to Cloud County; not found in winter in southwest by Schwilling.

Subspecies in Kansas: *M. e. erythrocephalus* (Linnaeus), intergrading in west with *M. e. caurinus* Brodkorb.

Asyndesmus lewis (Gray). Lewis Woodpecker. Possibly rare resident in southwest but status uncertain. Several specimens and sight records from western third of state; one specimen, female (KU 7890), from Lawrence, Douglas County, November 7, 1908, Bunker and Wetmore.

No subspecies recognized.

Sphyrapicus varius. Yellow-bellied Sapsucker. Uncommon transient and winter resident throughout state.

Subspecies in Kansas: *S. v. varius* (Linnaeus) in eastern Kansas, *S. v. nuchalis* Baird in western part (three specimens, Wallace and Morton counties).

[*Sphyrapicus thyroideus.* Williamson Sapsucker. An adult male seen at Concordia, Cloud County, April 4, 1935, by Dr. J. M. Porter. Placed in Hypothetical List in absence of a specimen.]

* *Dendrocopos villosus.* Hairy Woodpecker. Common resident throughout state.

Subspecies in Kansas: *D. v. villosus* (Linnaeus).

* *Dendrocopos pubescens.* Downy Woodpecker. Common resident throughout state.

Subspecies in Kansas: *D. p. pubescens* (Linnaeus) in southeast (Labette and Montgomery counties), *D. p. medianus* (Swainson) in rest of state, with fairly broad zone of intergradation between the two subspecies.

Dendrocopos scalaris. Ladder-backed Woodpecker. Common resident in extreme southwestern Kansas (Morton County). Six specimens. No nest found yet in Kansas.

Subspecies in Kansas: *D. s. symplectus* (Oberholser).

* *Tyrannus tyrannus* (Linnaeus). Eastern Kingbird. Common transient and summer resident throughout state; most numerous in east.

No subspecies recognized.

* *Tyrannus verticalis* Say. Western Kingbird. Common transient and summer resident east to Flint Hills; uncommon transient and summer resident in east (occurs regularly at Lawrence but rarely at Kansas City).

No subspecies recognized.

Tyrannus vociferans. Cassin Kingbird. Transient and summer resident in extreme western part, east to Finney County. One specimen: male, Kansas Highway 27 at Cimarron River [7½ miles north of Elkhart], Morton County, May 26, 1950, Richard and Jean Graber. No nesting record. Status poorly known.

Subspecies in Kansas: *T. v. vociferans* Swainson.

* *Muscivora forficata* (Gmelin). Scissor-tailed Flycatcher. Common summer resident in southern and central Kansas; nesting west to Morton County, north to Cloud County, east to Neosho County. Sporadic records elsewhere in state.

No subspecies recognized.

* *Myiarchus crinitus.* Crested Flycatcher. Common transient and summer resident throughout state, but perhaps less numerous in west.

Subspecies in Kansas: *M. c. boreus* Bangs.

Myiarchus cinerascens. Ash-throated Flycatcher. Known only from Morton County; several seen in May, 1950, and a female with somewhat enlarged ovary taken, 8 miles south of Richfield, May 7, 1950, Richard and Jean Graber. No nesting record.

Subspecies in Kansas: *M. c. cinerascens* (Lawrence).

* *Sayornis phoebe* (Latham). Eastern Phoebe. Common transient and summer resident in east; occurs, but must less common, in west.

No subspecies recognized.

* *Sayornis saya*. Say Phoebe. Common transient and summer resident in west. Nesting records from Rawlins, Jewell, Logan, and Ness counties. In migration, reported east to Republic and Lyon counties.

Subspecies in Kansas: *S. s. saya* (Bonaparte) is the breeding bird; *S. s. yukonensis* Bishop probably occurs in migration.

Empidonax flaviventris (Baird and Baird). Yellow-bellied Flycatcher. Uncommon transient in east. Specimens from Johnson, Douglas, and Shawnee counties.

No subspecies recognized.

* *Empidonax virescens* (Vieillot). Acadian Flycatcher. Summer resident in eastern Kansas. Specimens from Doniphan, Leavenworth, Douglas, Woodson, Montgomery, and Labette counties. Nesting records from Doniphan County (Jean M. Linsdale), Linn County (Wilson J. and Eunice Dingus), and Douglas County (R. F. Miller).

No subspecies recognized.

Empidonax traillii. Alder Flycatcher. Transient throughout state; no satisfactory nesting records or specimens taken in breeding season.

Subspecies in Kansas: *E. t. brewsteri* Oberholser transient, probably more common in west, and *E. t. traillii* (Audubon) transient and perhaps breeding in east.

Empidonax minimus (Baird and Baird). Least Flycatcher. Common transient throughout state; no satisfactory evidence of nesting.

No subspecies recognized.

Empidonax oberholseri Phillips. Wright Flycatcher. Known only from three specimens, May 8 (male and female) and May 12 (male), 1950, eight miles south of Richfield, Morton County, Richard and Jean Graber.

No subspecies recognized.

Empidonax difficilis. Western Flycatcher. Known only from two specimens taken eight miles south of Richfield, Morton County; September 3, 1952, immature female, Jean Graber; September 5, 1952, immature male (KU 31203), Richard Graber.

Subspecies in Kansas: *E. d. hellmayri* Brodkorb (female specimen); intermediate between *E. d. hellmayri* and *E. d. difficilis* Baird (male specimen).

* *Contopus virens* (Linnaeus). Eastern Wood Pewee. Common transient and summer resident in east, rare transient in west. Breeding distribution in state poorly known.

No subspecies recognized.

Contopus richardsonii. Western Wood Pewee. Common transient and probably summer resident in west; rare transient in east (specimen from Greenwood County and one seen in Cloud County). No nesting record.

Subspecies in Kansas: *C. r. richardsonii* (Swainson).

Nuttallornis borealis (Swainson). Olive-sided Flycatcher. Uncommon transient throughout state.

No subspecies recognized.

* *Eremophila alpestris.* Horned Lark. Common transient and resident throughout state. Numbers augmented by northern birds in winter.

Subspecies in Kansas: *E. a. praticola* (Henshaw) resident in east; *E. a. enthymia* (Oberholser) resident west of Flint Hills; *E. a. hoyti* (Bishop), *E. a. alpestris* (Linnaeus), and *E. a. leucolaema* (Coues) in winter.

[*Tachycineta thalassina.* Violet-green Swallow. Five birds seen at Lake Shawnee, Shawnee County, April 14, 1947, by L. B. Carson. Placed in Hypothetical List in absence of a specimen.]

* *Iridoprocne bicolor* (Vieillot). Tree Swallow. Summer resident in extreme northeastern Kansas; common transient throughout eastern half of state, status in west not known. Nesting records only from Doniphan County, along Missouri River, four nests located by Linsdale, in 1922, 1923, and 1924, and Leavenworth County, nests found by Brumwell along Missouri River.

No subspecies recognized.

* *Riparia riparia.* Bank Swallow. Common transient and summer resident, probably throughout state but status in northwest not known.

Subspecies in Kansas: *R. r. riparia* (Linnaeus).

* *Stelgidopteryx ruficollis.* Rough-winged Swallow. Common transient and summer resident throughout state.

Subspecies in Kansas: *S. r. serripennis* (Audubon).

* *Hirundo rustica.* Barn Swallow. Common transient and summer resident throughout state.

Subspecies in Kansas: *H. r. erythrogaster* Boddaert.

* *Petrochelidon pyrrhonota.* Cliff Swallow. Common transient and locally common summer resident throughout state.

Subspecies in Kansas: *P. p. pyrrhonota* (Vieillot).

* *Progne subis.* Purple Martin. Common transient and summer resident in east to uncommon or rare in west.

Subspecies in Kansas: *P. s. subis* (Linnaeus).

* *Cyanocitta cristata.* Blue Jay. Common transient and resident throughout state; less common in northern and western sections in winter.

Subspecies in Kansas: *C. c. bromia* Oberholser in east, *C. c. cyanotephra* Sutton in west, intergrading through central Kansas.

[*Cyanocitta stelleri.* Steller Jay. Several sight records from southwestern Kansas. Placed in Hypothetical List in absence of a specimen.]

Aphelocoma coerulescens. Scrub Jay. Irregular winter resident in southwestern Kansas. Five specimens (KU 20812-5, 21213), 12 miles northeast of Elkhart, Morton County, November 8, 10, 14, 1934, W. S. Long and Fred Hastie. Two seen in Finney County, January 15, 1955, by Marvin D. Schwilling.

Subspecies in Kansas: *A. c. woodhouseii* (Baird).

Aphelocoma ultramarina. Arizona Jay. Accidental. One specimen: "probably female," near Mt. Jesus, Clark County, March, 1906, B. Ashton Keith. Identification confirmed by L. L. Dyche; present location of specimen unknown.

Subspecies in Kansas: *A. u. arizonae* (Ridgway).

* *Pica pica.* American Magpie. Common resident in west; occasional in east in winter. Eastward extent of breeding range poorly known; nests from Ottawa (1951), Republic (1951 and 1953), and Cloud (1954) counties. Extending breeding range eastward (J. M. Porter).

Subspecies in Kansas: *P. p. hudsonia* (Sabine).

Corvus corax. American Raven. Formerly occurred on High Plains, precise status not known. No records since disappearance of bison herds. One specimen: Jewell County, date unknown, Edward Kern (specimen now at Kansas State College, Manhattan).

Subspecies in Kansas: *C. c. sinuatus* Wagler.

* *Corvus cryptoleucus* Couch. White-necked Raven. Common summer resident in western two tiers of counties; occasional resident east to Ford County. Locally common winter resident (Finney, Scott, and Sherman counties). One shot at Larned, Pawnee County, about October 25, 1937, by Frank Robl.

No subspecies recognized.

* *Corvus brachyrhynchos.* Crow. Common resident in east, less common in west. Abundant transient and winter resident in central Kansas.

Subspecies in Kansas: *C. b. brachyrhynchos* Brehm.

Gymnorhinus cyanocephalus Wied. Piñon Jay. Irregular winter visitant, more frequent in west than in east. Reported from Douglas (twice), Sedgwick, Mitchell, Clark, Finney, and Kearny counties.

No subspecies recognized.

Nucifraga columbiana (Wilson). Clark Nutcracker. Irregular winter visitant, more frequent in west than in east. Reported from Marshall (twice), Ellis, Lyon, Finney, and Seward counties.

No subspecies recognized.

* *Parus atricapillus.* Black-capped Chickadee. Common resident in entire state except for southern tier of counties, where either rare or absent in summer and locally common in winter.

Subspecies in Kansas: *P. a. atricapillus* Linnaeus in east, where most specimens are more or less intermediate toward *P. a. septentrionalis* Harris, the resident subspecies in the west.

* *Parus carolinensis.* Carolina Chickadee. Common resident in southern tier of counties; taken also in Greenwood County. Reported occurrence in Douglas County is erroneous. Proof of breeding rests on partly grown juveniles taken in Barber County, and on two nests found in Montgomery County by L. B. Carson.

Subspecies in Kansas: *P. c. atricapilloides* Lunk.

* *Parus bicolor* Linnaeus. Tufted Titmouse. Common resident in eastern Kansas, west at least to Barber, Harvey, and Cloud counties. Western limit of breeding range poorly known.

No subspecies recognized.

* *Sitta carolinensis.* White-breasted Nuthatch. Uncommon and local resident and winter visitant throughout state. Three positive nesting records, all from Douglas County, by C. D. Bunker, R. F. Miller, and Katherine Kelley.

Subspecies in Kansas: *S. c. carolinensis* Latham resident in Labette and Montgomery counties; *S. c. nelsoni* Mearns occurs in at least Morton County, status uncertain; *S. c. cookei* Oberholser resident and winter visitant in rest of state.

Sitta canadensis Linnaeus. Red-breasted Nuthatch. Uncommon transient and winter resident throughout state.

No subspecies recognized.

Certhia familiaris. Brown Creeper. Fairly common transient and winter resident throughout state.

Subspecies in Kansas: *C. f. americana* Bonaparte.

* *Troglodytes aëdon.* House Wren. Transient and summer resident, common in east to uncommon in west.

Subspecies in Kansas: *T. a. parkmanii* Audubon.

Troglodytes troglodytes. Winter Wren. Rare or uncommon transient and winter resident throughout state.

Subspecies in Kansas: *T. t. hiemalis* Vieillot.

* *Thryomanes bewickii.* Bewick Wren. Resident, common in south, rare in north; status poorly known. Nesting records from Shawnee, Johnson, and Montgomery counties.

Subspecies in Kansas: *T. b. bewickii* (Audubon) in northern and northeastern part, *T. b. cryptus* Oberholser in rest of state. (*T. b. niceae* Sutton, a questionably valid subspecies, has been reported from Meade and Morton counties.)

* *Thryothorus ludovicianus.* Carolina Wren. Resident, common in south, less common to north and west. One record from Hamilton County; status in northwest unknown.

Subspecies in Kansas: *T. l. ludovicianus* (Latham).

* *Telmatodytes palustris.* Long-billed Marsh Wren. Uncommon transient throughout state; known as a breeding bird only from Doniphan County, where Linsdale found several nests and collected a juvenile (KU 12869) with half-grown tail, August 31, 1922.

Subspecies in Kansas: *T. p. dissaëptus* (Bangs).

* *Cistothorus platensis.* Short-billed Marsh Wren. Uncommon transient and irregular summer resident in east, no records from west. One breeding record: male (KU 29665), female (KU 29666), and their nest with four eggs, eight miles west of Lawrence, Douglas County, August 30, 1950, H. B. Tordoff and G. P. Young.

Subspecies in Kansas: *C. p. stellaris* (Naumann).

* *Salpinctes obsoletus.* Rock Wren. Common transient and summer resident in west, rare transient in east; eastern limit of breeding range not known. Nests found in Hamilton, Scott, and Logan counties.

Subspecies in Kansas: *S. o. obsoletus* (Say).

* *Mimus polyglottos.* Mockingbird. Resident throughout state, less common in north, especially in winter.

Subspecies in Kansas: *M. p. polyglottos* (Linnaeus) in east, *M. p. leucopterus* (Vigors) in west (most specimens from Kansas are intermediate between the two subspecies).

* *Dumetella carolinensis* (Linnaeus). Catbird. Common transient and summer resident throughout state.

No subspecies recognized.

* *Toxostoma rufum.* Brown Thrasher. Common transient and summer resident throughout state; occasional winter resident at least in east.

Subspecies in Kansas: *T. r. rufum* (Linnaeus) in east, *T. r. longicauda* Baird in west.

Oreoscoptes montanus (Townsend). Sage Thrasher. Rare transient in west. Two unsexed specimens (KU 31941, 31942), 1 mile south of Holcomb, Finney County, September 20 and October 2, 1954, Marvin D. Schwilling. A third individual seen in Morton County, September 27, 1954, and a fourth in Kearny County, March 23, 1955, by Schwilling.

No subspecies recognized.

* *Turdus migratorius.* Robin. Common transient and summer resident; locally common winter resident.

Subspecies in Kansas: *T. m. migratorius* Linnaeus breeds in most of state but birds in southeast are intermediate toward *T. m. achrusterus* (Batchelder); *T. m. propinquus* Ridgway occurs in west, at least in migration, and irregularly in other parts of state in winter.

Ixoreus naevius. Varied Thrush. Accidental. One record: specimen (present location unknown) taken at Garden City, Finney County, October 17, 1891, H. W. Menke.

Subspecies in Kansas: Probably *I. n. meruloides* (Swainson), on geographical grounds.

* *Hylocichla mustelina* (Gmelin). Wood Thrush. Common transient and summer resident in east, absent in west, western limit of breeding in Kansas not known (nests, but uncommonly, in Cloud County).

No subspecies recognized.

Hylocichla guttata. Hermit Thrush. Transient throughout state, usually uncommon. Rare in winter in east.

Subspecies in Kansas: *H. g. faxoni* Bangs and Penard in east, *H. g. sequoiensis* (Belding) in west.

Hylocichla ustulata. Olive-backed Thrush. Common transient throughout state.

Subspecies in Kansas: *H. u. swainsoni* (Tschudi).

Hylocichla minima. Gray-cheeked Thrush. Fairly common transient in east; probably does not occur in west but western limit in migration in Kansas unknown (rare in Cloud County, three records by J. M. Porter).

Subspecies in Kansas: *H. m. minima* (Lafresnaye).

Hylocichla fuscescens. Veery. Transient, rare in east, fairly common in west.

Subspecies in Kansas: *H. f. salicicola* Ridgway.

* *Sialia sialis.* Eastern Bluebird. Common resident and transient throughout state.

Subspecies in Kansas: *S. s. sialis* (Linnaeus).

[*Sialia mexicana.* Chestnut-backed Bluebird. Said to be winter resident at Coolidge, Hamilton County, by Shanstrum. Reliably reported from southeastern Colorado. Placed in Hypothetical List in absence of a specimen from Kansas.]

Sialia currucoides (Bechstein). Mountain Bluebird. Common winter resident in west; occurs regularly east to Cloud and Barber counties and irregularly farther east (to Douglas and Anderson counties). Bunker and Rocklund took a full-grown juvenal female (KU 5900) on June 20, 1911, near the Colorado line northwest of Coolidge, Hamilton County.

No subspecies recognized.

Myadestes townsendi. Townsend Solitaire. Winter resident in small numbers in west; irregular in winter in east.

Subspecies in Kansas: *M. t. townsendi* (Audubon).

* *Polioptila caerulea.* Blue-gray Gnatcatcher. Common transient and summer resident in east, probably transient only in west but status there poorly known. Nesting records from Doniphan, Douglas, and Barber counties.

Subspecies in Kansas: *P. c. caerulea* (Linnaeus).

Regulus satrapa. Golden-crowned Kinglet. Common transient throughout state; uncommon winter resident.

Subspecies in Kansas: *R. s. satrapa* Lichtenstein.

Regulus calendula. Ruby-crowned Kinglet. Common transient throughout state; rare winter resident.

Subspecies in Kansas: *R. c. calendula* (Linnaeus).

Anthus spinoletta. Water Pipit. Common transient throughout state, more numerous in west.

Subspecies in Kansas: *A. s. rubescens* (Tunstall).

Anthus spraguei (Audubon). Sprague Pipit. Transient throughout state, perhaps more common in central or western parts; status poorly known. Specimens known from Trego, Cloud, Greenwood, Woodson, and Anderson counties.

No subspecies recognized.

Bombycilla garrulus. Bohemian Waxwing. Rare winter visitant throughout state. Few specimens on record, from Riley, Shawnee, Jefferson, Greenwood, and Sedgwick counties.

Subspecies in Kansas: *B. g. pallidiceps* Reichenow.

* *Bombycilla cedrorum* Vieillot. Cedar Waxwing. Common transient and irregular winter resident throughout state; rare summer resident in northeast. Breeding records: four nests found at Lake Quivira, Wyandotte County, July 22, 1947 (nestling collected, KU 32374), July 3, 1949 (young in nest), July 4, 1950, July 10, 1952 (young in nest), Harold C. Hedges; nest found in Topeka, Shawnee County, June 16, 1953, Cliff Olander and T. W. Nelson.

No subspecies recognized.

Lanius excubitor. Northern Shrike. Winter resident, rare in east, uncommon in west.

Subspecies in Kansas: *L. e. borealis* Vieillot in east, *L. e. invictus* Grinnell in west (most specimens from Kansas are intermediate between the two).

* *Lanius ludovicianus.* Loggerhead Shrike. Common resident and transient throughout state, but may leave north-central and northwestern parts in winter.

Subspecies in Kansas: *L. l. migrans* Palmer in extreme east, *L. l. excubitorides* Swainson in west, east to Norton, Ness, and Clark counties; birds from rest of state mostly intermediate.

* *Sturnus vulgaris.* Starling. Introduced. First appeared in early 1930's, now common transient and resident throughout state.

Subspecies in Kansas: *S. v. vulgaris* Linnaeus.

* *Vireo atricapillus* Woodhouse. Black-capped Vireo. Summer resident in Comanche and possibly other south-central counties. Status poorly known. Goss collected three pairs in southeastern Comanche County, May 7 to 18, 1885, and found a nest under construction on May 11, 1885. Sight records from Manhattan, Riley County, June 18, 1953, by Scott Searles, and Halstead, Harvey County, May 16, 1951, by Edna L. Ruth.

No subspecies recognized.

* *Vireo griseus.* White-eyed Vireo. Locally common transient and summer resident in east. Status poorly known. Nesting records from Doniphan County (Linsdale) and Kansas City region; specimens taken in summer from Douglas, Montgomery, and Labette counties.

Subspecies in Kansas: *V. g. noveboracensis* (Gmelin).

* *Vireo bellii.* Bell Vireo. Common summer resident throughout state.

Subspecies in Kansas: *V. b. bellii* Audubon.

* *Vireo flavifrons* Vieillot. Yellow-throated Vireo. Uncommon transient and local, uncommon summer resident throughout state. Goss reported two nests, one with 1 Cowbird and 3 vireo eggs, at Neosho Falls, Woodson County, May 9, 1877, and one under construction at Topeka, Shawnee County, May 18, 1883. T. W. Nelson found a nest at Topeka in 1947 (date approximate). R. F. Miller found an occupied nest 3 miles north of Baldwin, Douglas County, May 6, 1947.

No subspecies recognized.

Vireo solitarius. Solitary Vireo. Fairly common transient throughout state.

Subspecies in Kansas: *V. s. solitarius* (Wilson) in east, *V. s. plumbeus* Coues and *V. s. cassinii* Xantus in west.

* *Vireo olivaceus* (Linnaeus). Red-eyed Vireo. Common transient and summer resident throughout state.

No subspecies recognized.

Vireo philadelphicus (Cassin). Philadelphia Vireo. Uncommon transient in east (often overlooked); reported west to Harvey County but western limit of migration in Kansas not known.

No subspecies recognized.

* *Vireo gilvus.* Warbling Vireo. Common transient and summer resident throughout state.

Subspecies in Kansas: *V. g. gilvus* (Vieillot).

* *Mniotilta varia* (Linnaeus). Black and White Warbler. Common transient throughout state, local and uncommon summer resident in east. Breeding distribution in state poorly known. Nests reported in Douglas and Leavenworth counties.

No subspecies recognized.

* *Protonotaria citrea* (Boddaert). Prothonotary Warbler. Locally common transient and summer resident in eastern Kansas. Nesting records from Doniphan, Leavenworth, Johnson, Douglas, Shawnee, and Woodson counties.

No subspecies recognized.

* *Helmitheros vermivorus* (Gmelin). Worm-eating Warbler. Rare transient (specimens from Doniphan, Douglas, and Woodson counties) and summer resident in east. Linsdale saw a singing bird on July 11, 1923, in Doniphan County. Hilton (Wilson Bull., 32, 1920: 85-86) reports finding a newly-fledged young bird with an adult at Fort Leavenworth, Leavenworth County, on June 7, 1919 (some of Hilton's records seem highly improbable, but the one in question is convincing to me).

No subspecies recognized.

Vermivora chrysoptera (Linnaeus). Golden-winged Warbler. Rare transient in east. Several sight records and one specimen: female (KU 12700), 3 miles south of Lawrence, Douglas County, May 2, 1921, E. R. Hall.

No subspecies recognized.

Vermivora pinus (Linnaeus). Blue-winged Warbler. Uncommon transient in east. Possibly nests rarely but no definite evidence.

No subspecies recognized.

Vermivora peregrina (Wilson). Tennessee Warbler. Common transient in east, uncommon transient in west.

No subspecies recognized.

Vermivora celata. Orange-crowned Warbler. Common transient throughout state.

Subspecies in Kansas: *V. c. celata* (Say) throughout state, *V. c. orestera* Oberholser in west.

Vermivora ruficapilla. Nashville Warbler. Common transient throughout state.

Subspecies in Kansas: *V. r. ruficapilla* (Wilson).

Vermivora virginiae (Baird). Virginia Warbler. Transient in extreme west. Known in Kansas only from 8 miles south of Richfield, Morton County: five birds seen, two collected, May 4 to 10, 1950, Richard and Jean Graber.

No subspecies recognized.

* *Parula americana* (Linnaeus). Parula Warbler. Fairly common transient and local summer resident in eastern Kansas. Nesting records from Riley, Doniphan, Douglas, and Woodson counties; western limit of breeding distribution unknown.

No subspecies recognized.

* *Dendroica petechia.* Yellow Warbler. Common transient and summer resident throughout state.

Subspecies in Kansas: *D. p. aestiva* (Gmelin) breeding in all except southwestern Kansas; *D. p. sonorana* Brewster probably breeding in extreme southwest (specimens from Morton County); *D. p. rubiginosa* (Pallas) transient, probably throughout state.

Dendroica magnolia (Wilson). Magnolia Warbler. Uncommon transient throughout state.

No subspecies recognized.

Dendroica tigrina (Gmelin). Cape May Warbler. Rare transient in east. Several sight records but only one specimen from state: immature male (KU 31644), Lawrence, Douglas County, December 6, 1954 (abnormally late date), Mary Edith Kizer.

No subspecies recognized.

Dendroica caerulescens. Black-throated Blue Warbler. Rare transient, more records from west than from east.

Subspecies in Kansas: *D. c. caerulescens* (Gmelin).

Dendroica coronata. Myrtle Warbler. Common transient throughout state, rare winter resident. (See also Audubon Warbler.)

Subspecies in Kansas: *D. c. coronata* (Linnaeus) and *D. c. hooveri* McGregor.

Dendroica auduboni. Audubon Warbler. Common transient in west, rare in east, specimens taken east to Trego County. Hybrids between this species and Myrtle Warbler common in west.

Subspecies in Kansas: *D. a. auduboni* (Townsend).

Dendroica nigrescens (Townsend). Black-throated Gray Warbler. Common transient in extreme western Kansas. Several sight records and four specimens from 8 miles south of Richfield, Morton County, May 8 to 13, 1950, Richard and Jean Graber.

No subspecies recognized.

Dendroica townsendi (Townsend). Townsend Warbler. Transient in extreme western Kansas. Five records: all from 8 miles south of Richfield, Morton County, May 3 (female collected), 11, and 20, 1950, September 3 and 5 (immature female, KU 31206), 1952, Richard and Jean Graber.

No subspecies recognized.

Dendroica virens. Black-throated Green Warbler. Transient, uncommon in east and rare in west.

Subspecies in Kansas: *D. v. virens* (Gmelin).

Dendroica cerulea (Wilson). Cerulean Warbler. Uncommon transient and possibly summer resident in east, but status poorly known. No definite nesting record. Only five specimens on record.

No subspecies recognized.

Dendroica fusca (Müller). Blackburnian Warbler. Transient, uncommon in east, rare in west.

No subspecies recognized.

[*Dendroica dominica.* Sycamore Warbler. A few sight records from east and possibly breeds in southeast but placed on Hypothetical List until a specimen from state is obtained.]

Dendroica pensylvanica (Linnaeus). Chestnut-sided Warbler. Transient, fairly common in east, uncommon in west. Only three specimens from state, two from Shawnee County, one from Morton County.

No subspecies recognized.

Dendroica castanea (Wilson). Bay-breasted Warbler. Uncommon transient throughout state.

No subspecies recognized.

Dendroica striata (Forster). Black-poll Warbler. Common transient in east, uncommon or rare in west.

No subspecies recognized.

[*Dendroica pinus.* Pine Warbler. Probably rare transient in east where several have been reported seen, but placed in Hypothetical List in absence of a specimen from Kansas. Linsdale reported taking a Pine Warbler in Doniphan County, September 13, 1923, but the specimen is actually a Cerulean Warbler.]

* *Dendroica discolor.* Prairie Warbler. Known to occur regu-

larly only in Wyandotte and Johnson counties, where locally common transient and summer resident; newly fledged young have been found. One specimen: male (KU 32376), 2 miles west of Lake Quivira, Johnson County, May 3, 1942, Harold C. Hedges.

Subspecies in Kansas: *D. d. discolor* (Vieillot).

Dendroica palmarum. Palm Warbler. Uncommon transient in east, west at least to Cloud County. Western limit of occurrence in migration not known.

Subspecies in Kansas: *D. p. palmarum* (Gmelin).

* *Seiurus aurocapillus.* Oven-bird. Fairly common transient throughout state; local summer resident in northeast. Brumwell reported one pair nesting in June, 1939, and in 1940, at Fort Leavenworth, Leavenworth County. His report is lacking in details but no other nesting records are available.

Subspecies in Kansas: *S. a. aurocapillus* (Linnaeus) throughout state, *S. a. cinereus* A. H. Miller taken in Cheyenne County.

Seiurus noveboracensis. Northern Water-thrush. Fairly common transient throughout state.

Subspecies in Kansas: *S. n. notabilis* Ridgway.

* *Seiurus motacilla* (Vieillot). Louisiana Water-thrush. Fairly common transient and summer resident in east, uncommon transient in west. Approximately 11 breeding records, all from Miami and Linn counties. Summer distribution in state inadequately known.

No subspecies recognized.

* *Oporornis formosus* (Wilson). Kentucky Warbler. Common transient and summer resident in east. Nests west to Riley County, but not reported from Cloud County by Porter.

No subspecies recognized.

Oporornis philadelphia (Wilson). Mourning Warbler. Locally common transient in east, west rarely to Sedgwick and Cloud counties. Sight records supposedly of Connecticut Warblers (*Oporornis agilis*) may, at least in part, refer to this species. No specimens of *O. agilis* known from state.

No subspecies recognized.

Oporornis tolmiei. Macgillivray Warbler. Common transient in extreme western Kansas, accidental in east. Specimens from Morton, Hamilton, and Marshall (1) counties.

Subspecies in Kansas: *O. t. monticola* Phillips.

* *Geothlypis trichas.* Yellow-throat. Common transient throughout state; common summer resident in east, less common in west.

Subspecies in Kansas: *G. t. brachidactyla* (Swainson) breeds in east; *G. t. occidentalis* Brewster breeds in west. Distribution in Kansas of these subspecies and identity of transients poorly known.

* *Icteria virens.* Yellow-breasted Chat. Common transient and summer resident, perhaps less common in west.

Subspecies in Kansas: *I. v. virens* (Linnaeus) in east, *I. v. auricollis* (Lichtenstein) in west, intergrading through most of state.

Wilsonia citrina (Boddaert). Hooded Warbler. Formerly common summer resident in east, now rare and perhaps no longer nests in state. No satisfactory breeding record. Three males from Leavenworth County, May 9, 1871, and one from Shawnee County, May 17, 1871, taken by J. A. Allen, are now at Harvard.

No subspecies recognized.

Wilsonia pusilla. Wilson Warbler. Common transient throughout state.

Subspecies in Kansas: *W. p. pusilla* (Wilson) in east, *W. p. pileolata* (Pallas) in west; precise distribution in migration unknown.

Wilsonia canadensis (Linnaeus). Canada Warbler. Uncommon transient in east, reported west to Sedgwick and Cloud counties.

No subspecies recognized.

* *Setophaga ruticilla.* American Redstart. Common transient and local summer resident in east; probably only transient in west but breeding range in state poorly known. Few definite nesting records: Brumwell reported nesting at Fort Leavenworth, Leavenworth County; J. M. Porter found a nest in Republic County, May 22, 1940.

Subspecies in Kansas: *S. r. ruticilla* (Linnaeus) is breeding form; *S. r. tricolora* (Müller) occurs in migration.

* *Passer domesticus.* English Sparrow. Introduced. Common resident throughout state.

Subspecies in Kansas: *P. d. domesticus* (Linnaeus).

* *Dolichonyx oryzivorus* (Linnaeus). Bobolink. Transient, uncommon in east and rare in west in spring; rare in east and absent in west in fall. In 1940, several pairs remained until July 21 near Jamestown State Lake, Cloud County, and two pairs were seen feeding fledglings on June 25 (J. M. Porter). No other good evidence of breeding.

No subspecies recognized.

* *Sturnella magna.* Eastern Meadowlark. Common transient and resident in eastern part. Nests locally west to Jewell County in north and Barber County in south. Less common in winter.

Subspecies in Kansas: *S. m. magna* (Linnaeus) in northeast, *S. m. argutula* Bangs in southeast.

* *Sturnella neglecta.* Western Meadowlark. Common transient and resident in western part. Nests commonly east to Flint Hills, irregularly and uncommonly in east. Largely replaces Eastern Meadowlark in east in winter.

Subspecies in Kansas: *S. n. neglecta* Audubon.

* *Xanthocephalus xanthocephalus* (Bonaparte). Yellow-headed Blackbird. Transient, common in west and uncommon in east, and uncommon, local summer resident. Breeds more frequently in west; nesting records from Meade, Wallace, Barton, Stafford, Doniphan, and Douglas counties. One winter record, Riley County.

No subspecies recognized.

* *Agelaius phoeniceus.* Red-wing. Common transient and summer resident throughout state, less common winter resident.

Subspecies in Kansas: *A. p. phoeniceus* (Linnaeus) breeds in most of state; *A. p. fortis* Ridgway may nest in west and occurs in migration; *A. p. arctolegus* Oberholser occurs in migration.

* *Icterus spurius* (Linnaeus). Orchard Oriole. Common transient and summer resident throughout state.

No subspecies recognized.

Icterus cucullatus. Hooded Oriole. Accidental. One record: bird banded at Los Angeles, California, January 22, 1939, found dead by Dr. F. S. Williams, 16 miles southeast of Garden City, Finney County, about August 5, 1939; foot of specimen preserved.

Subspecies in Kansas: *I. c. californicus* (Lesson), on geographic grounds.

* *Icterus galbula* (Linnaeus). Baltimore Oriole. Common transient and summer resident through most of state; hybridizes freely with Bullock Oriole in west. One winter record: immature male (KU 31988), Lawrence, Douglas County, December 25, 1953, H. B. Tordoff.

No subspecies recognized.

* *Icterus bullockii.* Bullock Oriole. Common transient and summer resident in west, rarely east to Stafford County (breeding?) and Douglas County (transient).

Subspecies in Kansas: *I. b. bullockii* (Swainson).

Euphagus carolinus. Rusty Blackbird. Common transient and locally common winter resident throughout state.

Subspecies in Kansas: *E. c. carolinus* (Müller).

Euphagus cyanocephalus (Wagler). Brewer Blackbird. Transient and local winter resident. Common in west, uncommon in east. Probably nests in northwest, but no satisfactory evidence of this.

No subspecies recognized.

* *Quiscalus quiscula.* Bronzed Grackle. Common transient and summer resident throughout state; local winter resident.

Subspecies in Kansas: *Q. q. versicolor* Vieillot.

* *Molothrus ater.* Cowbird. Common transient and summer resident throughout state; local winter resident.

Subspecies in Kansas: *M. a. ater* (Boddaert) is breeding bird; *M. a. artemisiae* Grinnell transient, common in west and possibly nesting in northwest.

Piranga ludoviciana (Wilson). Western Tanager. Fairly common transient and perhaps summer resident in extreme west. Two males taken 4½ miles west of Kendall, Hamilton County, May 20 and June 1, 1893, H. W. Menke; many seen and two males and a female (KU 31207) taken 8 miles south of Richfield, Morton County, May 6, 1950 (males) and September 4, 1952, Richard and Jean Graber.

No subspecies recognized.

* *Piranga olivacea* (Gmelin). Scarlet Tanager. Fairly common transient in east and uncommon summer resident in northeast. Distribution in state poorly known; breeding records from Doniphan, Leavenworth, and Cloud counties.

No subspecies recognized.

* *Piranga rubra.* Summer Tanager. Common transient and summer resident, distribution poorly known. Recorded in migration (possibly breeding?) west to Morton County and breeding in Doniphan and Douglas counties. Not reported by Porter as nesting in Cloud County.

Subspecies in Kansas: *P. r. rubra* (Linnaeus).

* *Richmondena cardinalis.* Cardinal. Common resident in east, uncommon in west, rare in extreme southwest.

Subspecies in Kansas: *R. c. cardinalis* (Linnaeus).

* *Pheucticus ludovicianus* (Linnaeus). Rose-breasted Grosbeak. Common transient and locally common summer resident in east. Reported in summer west to Rawlins County; probably absent in summer from southeast. Distribution poorly known.

No subspecies recognized.

* *Pheucticus melanocephalus.* Black-headed Grosbeak. Common transient and summer resident in west, nesting east to Cloud and Harvey counties. Occasionally occurs farther east in migration.

Subspecies in Kansas: *P. m. melanocephalus* (Swainson).

* *Guiraca caerulea.* Blue Grosbeak. Common transient and summer resident in most of state; locally common in summer in northeast.

Subspecies in Kansas: *G. c. caerulea* (Linnaeus) in east, *G. c. interfusa* Dwight and Griscom in west; most specimens from state are intergrades.

* *Passerina cyanea* (Linnaeus). Indigo Bunting. Common transient and summer resident west to Finney County, status in extreme west not known but probably absent there.

No subspecies recognized.

Passerina amoena (Say). Lazuli Bunting. Common transient and probably summer resident in extreme western Kansas. No breeding record. Rare in east in migration.

No subspecies recognized.

* *Passerina ciris.* Painted Bunting. Fairly common summer resident in east, west to Barber and north to Riley and Shawnee counties. One positive nesting record: nest with young, successfully fledged, Lawrence, Douglas County, spring and summer, 1918, Bessie D. Reed.

Subspecies in Kansas: *P. c. pallidior* Mearns.

* *Spiza americana* (Gmelin). Dickcissel. Transient and summer resident throughout state; common in east, locally common in west.

No subspecies recognized.

Hesperiphona vespertina. Evening Grosbeak. Rare and irregular winter visitant. Reported from widely scattered localities throughout state.

Subspecies in Kansas: *H. v. vespertina* (Cooper); *H. v. brooksi* Grinnell may occur in west.

Carpodacus purpureus. Purple Finch. Fairly common transient and winter resident in east; status in west not known.

Subspecies in Kansas: *C. p. purpureus* (Gmelin).

Carpodacus mexicanus. House Finch. Occurs in southwestern Kansas, reported common north to Hamilton County and east to Finney County. One record from Concordia, Cloud County, 2 or 3 birds seen from February 26 to March 6, 1954, Lillie and Ida Cook, J. M. Porter. Most records in winter; status in summer uncertain.

Subspecies in Kansas: *C. m. frontalis* (Say).

[*Pinicola enucleator.* Pine Grosbeak. One old record (possibly based on a specimen, but convincing details are lacking) and a few recent sight records from east. Placed in Hypothetical List in absence of an authentic specimen from state.]

Acanthis flammea. Redpoll. Rare and irregular winter visitant. Records from Cloud, Riley (specimen), Douglas (specimens), and Woodson counties, and Kansas City region.

Subspecies in Kansas: *A. f. flammea* (Linnaeus).

* *Spinus pinus.* Pine Siskin. Common but irregular transient and winter resident throughout state. Two breeding records: nest with 3 or 4 young, later successfully fledged, Onaga, Pottawatomie

County, May 3, 1920, F. F. Crevecoeur; nest with 3 eggs (young successfully fledged), 1 mile southwest of Concordia, Cloud County, observed from April 6 to 30, 1954, J. M. Porter.

Subspecies in Kansas: *S. p. pinus* (Wilson).

* *Spinus tristis.* Eastern Goldfinch. Common resident throughout state.

Subspecies in Kansas: *S. t. tristis* (Linnaeus).

* *Loxia curvirostra.* Red Crossbill. Irregular winter visitant throughout state, locally common at times. One nesting record: nest with one egg, Topeka, Shawnee County, March 22, 1917, A. Sidney Hyde. This nest later held three eggs, all hatched, three young fledged, and the family left the area in June.

Subspecies in Kansas (in approximate decreasing order of frequency): *L. c. benti* Griscom, *L. c. bendirei* Ridgway, *L. c. minor* (Brehm), *L. c. stricklandi* Ridgway, *L. c. sitkensis* Grinnell.

Loxia leucoptera. White-winged Crossbill. Rare and irregular winter visitant throughout the state. Only two specimens taken (Douglas and Ellis counties).

Subspecies in Kansas: *L. l. leucoptera* Gmelin.

Chlorura chlorura (Audubon). Green-tailed Towhee. Fairly common transient in west; rare winter visitant in east (Shawnee County, Wyandotte County).

No subspecies recognized.

* *Pipilo erythrophthalmus.* Red-eyed Towhee. Common transient and winter resident throughout state; uncommon summer resident in east, status in west in summer not known. No nest found, but recently fledged young reported in several counties.

Subspecies in Kansas: *P. e. erythrophthalmus* (Linnaeus) resident; *P. e. arcticus* (Swainson) winter resident throughout state; *P. e. montanus* Swarth reported as transient only from Morton County.

* *Calamospiza melanocorys* Stejneger. Lark Bunting. Common transient and summer resident in west, rare transient in east. Nesting in southwestern Kansas irregular; absent some years and present in other years. One nesting record from east, in Franklin County.

No subspecies recognized.

Passerculus sandwichensis. Savannah Sparrow. Common transient and rare winter resident throughout state.

Subspecies in Kansas: *P. s. savanna* (Wilson), *P. s. nevadensis* Grinnell, *P. s. oblitus* Peters and Griscom.

* *Ammodramus savannarum.* Grasshopper Sparrow. Common transient and local summer resident throughout state.

Subspecies in Kansas: *A. s. perpallidus* (Coues).

Ammodramus bairdii (Audubon). Baird Sparrow. One record:

male? (U. S. Natl. Mus. 155884), Pendennis, Lane County, April 25, 1897, J. A. Loring. This species probably occurs regularly in the state but is overlooked.

No subspecies recognized.

Passerherbulus caudacutus (Latham). Leconte Sparrow. Common transient and irregular, locally common winter resident west at least to Lane County.

No subspecies recognized.

* *Passerherbulus henslowii.* Henslow Sparrow. Uncommon transient and uncommon, local summer resident in east, west at least to Cloud County. Breeding records from Morris, Shawnee, Douglas, and Anderson counties.

Subspecies in Kansas: *P. h. henslowii* (Audubon).

Ammospiza caudacuta. Sharp-tailed Sparrow. Rare transient in east. Specimens taken in Shawnee, Douglas, Woodson, and McPherson counties. Supposed nesting reported by Goss probably erroneous.

Subspecies in Kansas: *A. c. nelsoni* (Allen).

Pooecetes gramineus. Vesper Sparrow. Common transient throughout state. May nest in northwest but no evidence available.

Subspecies in Kansas: *P. g. gramineus* (Gmelin) in east, *P. g. confinis* Baird in west.

* *Chondestes grammacus.* Lark Sparrow. Common transient and summer resident throughout state.

Subspecies in Kansas: *C. g. grammacus* (Say) east of Flint Hills, *C. g. strigatus* Swainson in west; the two subspecies intergrade in central Kansas.

Aimophila ruficeps. Rufous-crowned Sparrow. Two records: male (KU 29222), Schwarz Canyon, Comanche County, June 7, 1936, C. W. Hibbard; one seen near Point Rock, Morton County, May 21, 1950, Richard and Jean Graber.

Subspecies in Kansas: *A. r. scottii* (Sennett).

Aimophila aestivalis. Pine-woods Sparrow. One specimen: male (KU 32377), Lake Quivira, in Wyandotte County, April 26, 1948, Harold C. Hedges. One seen, Lake Quivira, in Johnson County, April 24, 1949, Harold C. Hedges.

Subspecies in Kansas: *A. a. illinoensis* (Ridgway).

* *Aimophila cassinii* (Woodhouse). Cassin Sparrow. Common summer resident in southwestern Kansas, known north to Hamilton County and east to Finney County. One nesting record: nest with two young and one pipped egg, one mile south of Garden City, Finney County, May 24, 1954, Marvin D. Schwilling.

No subspecies recognized.

Amphispiza bilineata. Black-throated Sparrow. One record: specimen of unknown sex (KU 31356), 4 miles north and 3 miles east of Garden City, Finney County, November 25, 1952, Marvin D. Schwilling.

Subspecies in Kansas: *A. b. deserticola* Ridgway.

Junco aikeni Ridgway. White-winged Junco. Fairly common transient and winter resident in western Kansas. Specimens from Wallace, Ellis, Hamilton, and Morton counties.

No subspecies recognized.

Junco hyemalis. Slate-colored Junco. Common transient and winter resident throughout state.

Subspecies in Kansas: *J. h. hyemalis* (Linnaeus), *J. h. cismontanus* Dwight.

Junco oreganus. Oregon Junco. Common transient and winter resident in west, uncommon in east.

Subspecies in Kansas: *J. o. montanus* Ridgway, *J. o. mearnsi* Ridgway.

Spizella arborea. Tree Sparrow. Common transient and winter resident throughout state.

Subspecies in Kansas: *S. a. arborea* (Wilson) common in east; *S. a. ochracea* Brewster common throughout state.

* *Spizella passerina.* Chipping Sparrow. Common transient and summer resident in east, less common in west. Only two actual nesting records: occupied nest at Lawrence, Douglas County, May, 1954, James S. Findley; nest with 4 large young, 6 miles south of Atchison, Atchison County, May, 1934 or 1935, Homer A. Stephens (photographs taken of nest and adult).

Subspecies in Kansas: *S. p. passerina* (Bechstein) in east, *S. p. arizonae* Coues in west.

Spizella pallida (Swainson). Clay-colored Sparrow. Common transient throughout state. Possibly breeds in northwest: male (KU 31950) with greatly enlarged testes (9 x 6 mm.), 1 mile north of St. Francis, Cheyenne County, June 12, 1954, H. B. Tordoff.

No subspecies recognized.

Spizella breweri. Brewer Sparrow. Common transient in west. Five specimens known: four males, Morton County, April 8 to May 1, 1950, Richard and Jean Graber; one specimen (sex?), Finney County, May 3, 1954, Marvin D. Schwilling.

Subspecies in Kansas: *S. b. breweri* Cassin.

* *Spizella pusilla.* Field Sparrow. Common transient and summer resident and uncommon winter resident throughout state.

Subspecies in Kansas: *S. p. arenacea* Chadbourne, intergrading in east with *S. p. pusilla* (Wilson).

Zonotrichia querula (Nuttall). Harris Sparrow. Common transient and winter resident in east, uncommon in west.

No subspecies recognized.

Zonotrichia leucophrys. White-crowned Sparrow. Common transient and winter resident throughout state.

Subspecies in Kansas: *Z. l. leucophrys* (Forster) common in east, uncommon in west; *Z. l. gambelii* (Nuttall) common in west, fairly common in east.

Zonotrichia albicollis (Gmelin). White-throated Sparrow. Fairly common transient, uncommon winter resident west at least to Cloud and Sedgwick counties. Status in west poorly known; not reported at Garden City by Marvin D. Schwilling.

No subspecies recognized.

Passerella iliaca. Fox Sparrow. Fairly common transient and uncommon winter resident in east; probably occurs in west but status there poorly known.

Subspecies in Kansas: *P. i. iliaca* (Merrem); other subspecies may be found in west when specimens become available.

Melospiza lincolnii. Lincoln Sparrow. Common transient and uncommon winter resident throughout state.

Subspecies in Kansas: *M. l. lincolnii* (Audubon) throughout state; *M. l. alticola* (Miller and McCabe) in extreme west.

Melospiza georgiana. Swamp Sparrow. Common transient and uncommon winter resident in east. Western limit of range in Kansas not known (rare transient in Cloud and Finney counties—Porter and Schwilling).

Subspecies in Kansas: *M. g. georgiana* (Latham), *M. g. ericrypta* Oberholser.

Melospiza melodia. Song Sparrow. Common transient and winter resident throughout state.

Subspecies in Kansas: *M. m. euphonia* Wetmore, *M. m. juddi* Bishop, *M. m. montana* Henshaw.

Rhynchophanes mccownii (Lawrence). McCown Longspur. Transient, common in west, rare in east, and winter resident, uncommon in west, rare in east.

No subspecies recognized.

Calcarius lapponicus. Lapland Longspur. Common transient and winter resident throughout state.

Subspecies in Kansas: *C. l. lapponicus* (Linnaeus) is the common form; *C. l. alascensis* Ridgway occurs uncommonly (specimens from Douglas and Hamilton counties).

Calcarius pictus (Swainson). Smith Longspur. Fairly common transient and locally common winter resident except in extreme east, where rare.

No subspecies recognized.

* *Calcarius ornatus* (Townsend). Chestnut-collared Longspur. Common transient and winter resident in west, uncommon in east. Formerly, at least, occurred in summer in High Plains of west; nests found in Ellis County in 1871 by J. A. Allen. No recent records in summer.

No subspecies recognized.

Plectrophenax nivalis. Snow Bunting. Winter visitant at irregular and, sometimes, long intervals. No specimens preserved in state since 1879.

Subspecies in Kansas: *P. n. nivalis* (Linnaeus).

Transmitted May 19, 1955.

Index to Common Names

Acadian Flycatcher, 334
Alder Flycatcher, 334
American Bittern, 312
American Coot, 322
American Egret, 311
American Knot, 325
American Magpie, 336
American Merganser, 317
American Raven, 336
American Redstart, 346
American Woodcock, 323
Arizona Jay, 336
Ash-throated Flycatcher, 333
Audubon Warbler, 343
Avocet, 326

Baird Sandpiper, 325
Baird Sparrow, 350
Bald Eagle, 319
Baldpate, 315
Baltimore Oriole, 347
Bank Swallow, 335
Barn Owl, 330
Barn Swallow, 335
Barred Owl, 330
Bay-breasted Warbler, 344
Bell Vireo, 341
Belted Kingfisher, 331
Bewick Wren, 338
Black and White Warbler, 342
Black-bellied Plover, 323
Black-billed Cuckoo, 329
blackbirds, 346-348
Blackburnian Warbler, 344
Black-capped Chickadee, 337
Black-capped Vireo, 341
Black-crowned Night Heron, 312
Black Duck, 314
Black-headed Grosbeak, 348
Black-necked Stilt, 326
Black-poll Warbler, 344
Black Rail, 322
Black Tern, 328
Black-throated Blue Warbler, 343
Black-throated Gray Warbler, 344
Black-throated Green Warbler, 344
Black-throated Sparrow, 352
Black Vulture, 318
Blue Goose, 314
Blue-gray Gnatcatcher, 340
Blue Grosbeak, 348
Blue Jay, 336
Blue-winged Teal, 315
Blue-winged Warbler, 342
Bobolink, 346
Bob-white, 321
Bohemian Waxwing, 340
Bonaparte Gull, 328
Brant, 314
Brewer Blackbird, 347
Brewer Sparrow, 352
Broad-winged Hawk, 319
Bronzed Grackle, 348
Brown Creeper, 337
Brown Pelican, 311
Brown Thrasher, 338
Buff-breasted Sandpiper, 326
Buffle-head, 316
Bullock Oriole, 347
buntings, 348-354
Burrowing Owl, 330

California Gull, 327
Calliope Hummingbird, 331
Canada Goose, 313
Canada Warbler, 346
Canvas-back, 316
Cape May Warbler, 343
Cardinal, 348
Carolina Chickadee, 337
Carolina Paroquet, 329
Carolina Wren, 338
Caspian Tern, 328
Cassin Kingbird, 333
Cassin Sparrow, 351
Catbird, 338
Cedar Waxwing, 340
Cerulean Warbler, 344
Chestnut-backed Bluebird, 339
Chestnut-collared Longspur, 354
Chestnut-sided Warbler, 344
chickadees, 337
Chimney Swift, 331
Chipping Sparrow, 352
Chuck-will's-widow, 331
Cinnamon Teal, 315
Clark Nutcracker, 337
Clay-colored Sparrow, 352
Cliff Swallow, 335
Common Loon, 310
Common Scoter, 317
Common Tern, 328
Cooper Hawk, 318
cormorants, 311
corvids, 336-337
Cowbird, 348
cranes, 321
Crested Flycatcher, 333
crossbills, 350
Crow, 336
cuckoos, 329-330

Dickcissel, 349
Double-crested Cormorant, 311
doves, 328-329
Downy Woodpecker, 333
Duck Hawk, 320
ducks, 314-317

eagles, 319
Eared Grebe, 310
Eastern Bluebird, 339
Eastern Goldfinch, 350
Eastern Kingbird, 333
Eastern Meadowlark, 346
Eastern Phoebe, 334
Eastern Wood Pewee, 335
Eider, 316
English Sparrow, 346
Eskimo Curlew, 324
European Widgeon, 315
Evening Grosbeak, 349

falcons, 320
Ferruginous Rough-leg, 319
Field Sparrow, 352
finches, 348-354
Flamingo, 313
Florida Gallinule, 322
flycatchers, 333-335
Forster Tern, 328
Fox Sparrow, 353
Franklin Gull, 327
Fulvous Tree-duck, 314

Gadwall, 315
geese, 313-314
Glaucous Gull, 327
goatsuckers, 331
Golden-crowned Kinglet, 340
Golden Eagle, 319
Golden-eye, 316
Golden Plover, 323
Golden-winged Warbler, 342
Goshawk, 318
Grasshopper Sparrow, 350
Gray-cheeked Thrush, 339
Great Blue Heron, 311
Greater Prairie Chicken, 320
Greater Scaup Duck, 316
Greater Yellow-legs, 325
grebes, 310
Green Heron, 312
Green-tailed Towhee, 350
Green-winged Teal, 315
Groove-billed Ani, 330
grosbeaks, 348-349
Ground Dove, 329
grouse, 320-321
gulls, 327-328
Gyrfalcon, 320

Hairy Woodpecker, 333
Harris Hawk, 319
Harris Sparrow, 353
Hawk Owl, 330
hawks, 318-320
Henslow Sparrow, 351
Hermit Thrush, 339
herons, 311-312
Herring Gull, 327
Hooded Merganser, 317
Hooded Oriole, 347
Hooded Warbler, 346
Horned Grebe, 310
Horned Lark, 335
Horned Owl, 330
House Finch, 349
House Wren, 337
Hudsonian Curlew, 324
Hudsonian Godwit, 326
hummingbirds, 331

ibises, 312-313
Inca Dove, 329
Indigo Bunting, 349

jaegers, 327
jays, 336-337
juncos, 352

Kentucky Warbler, 345
Killdeer, 323
King Eider, 316
kingfisher, 331
kinglets, 340
King Rail, 321
kites, 318
Kittiwake, 328

Ladder-backed Woodpecker, 333
Lapland Longspur, 353
lark, 335
Lark Bunting, 350
Lark Sparrow, 351
Laughing Gull, 327
Lazuli Bunting, 349
Least Bittern, 312
Least Flycatcher, 334
Least Sandpiper, 325
Least Tern, 328
Leconte Sparrow, 351
Lesser Prairie Chicken, 320
Lesser Scaup Duck, 316
Lesser Yellow-legs, 325
Lewis Woodpecker, 332
Lincoln Sparrow, 353
Little Blue Heron, 312
Loggerhead Shrike, 341
Long-billed Curlew, 324
Long-billed Dowitcher, 325
Long-billed Marsh Wren, 338
Long-eared Owl, 330
longspurs, 353-354
Long-tailed Jaeger, 327
loons, 310
Louisiana Heron, 312
Louisiana Water-thrush, 345

Macgillivray Warbler, 345
Magnolia Warbler, 343
magpie, 336
Mallard, 314
Man-o'-war-bird, 311
Marbled Godwit, 326
Marsh Hawk, 320
McCown Longspur, 353
meadowlarks, 346-347

Mexican Cormorant, 311
Mississippi Kite, 318
Mockingbird, 338
Mottled Duck, 314
Mountain Bluebird, 340
Mountain Plover, 323
Mourning Dove, 329
Mourning Warbler, 345
Myrtle Warbler, 343

Nashville Warbler, 343
Nighthawk, 331
Northern Phalarope, 327
Northern Shrike, 341
Northern Water-thrush, 345
nuthatches, 337

Old-squaw, 316
Olive-backed Thrush, 339
Olive-sided Flycatcher, 335
Orange-crowned Warbler, 343
Orchard Oriole, 347
Oregon Junco, 352
orioles, 347
Osprey, 320
Oven-bird, 345
owls, 330-331

Painted Bunting, 349
Palm Warbler, 345
Parula Warbler, 343
Passenger Pigeon, 329
Pectoral Sandpiper, 325
pelicans, 311
phalaropes, 326-327
Philadelphia Vireo, 342
Pied-billed Grebe, 310
Pigeon Hawk, 320
pigeons, 328-329
Pileated Woodpecker, 332
Pine Grosbeak, 349
Pine Siskin, 349
Pine Warbler, 344
Pine-woods Sparrow, 351
Piñon Jay, 337
Pintail, 315
Piping Plover, 323
pipits, 340
plovers, 323
Pomarine Jaeger, 327
Poor-will, 331
Prairie Falcon, 320
Prairie Warbler, 344
Prothonotary Warbler, 342
Purple Finch, 349
Purple Gallinule, 322
Purple Martin, 336

quail, 321

rails, 321-322
ravens, 336
Red-backed Sandpiper, 325
Red-bellied Woodpecker, 332
Red-breasted Merganser, 317
Red-breasted Nuthatch, 337
Red Crossbill, 350
Red-eyed Towhee, 350
Red-eyed Vireo, 342
Redhead, 315
Red-headed Woodpecker, 332
Red-necked Grebe, 310
Red Phalarope, 326
Redpoll, 349
Red-shafted Flicker, 332
Red-shouldered Hawk, 318
Red-tailed Hawk, 318
Red-throated Loon, 310
Red-wing, 347
Ring-billed Gull, 327
Ring-necked Duck, 316
Ring-necked Pheasant, 321
Road-runner, 329
Robin, 339
Rock Dove, 328
Rock Wren, 338
Roseate Spoonbill, 313
Rose-breasted Grosbeak, 348
Ross Goose, 314
Rough-legged Hawk, 319
Rough-winged Swallow, 335
Ruby-crowned Kinglet, 340
Ruby-throated Hummingbird, 331
Ruddy Duck, 317
Ruddy Turnstone, 323
Ruffed Grouse, 320
Rufous-crowned Sparrow, 351
Rusty Blackbird, 347

Sabine Gull, 328
Sage Thrasher, 338
Sanderling, 326
Sandhill Crane, 321
sandpipers, 323-326
Savannah Sparrow, 350
Saw-whet Owl, 330
Say Phoebe, 334
Scaled Quail, 321
Scarlet Tanager, 348
Scissor-tailed Flycatcher, 333
Screech Owl, 330
Scrub Jay, 336
Semipalmated Plover, 323
Semipalmated Sandpiper, 325
Sharp-shinned Hawk, 318
Sharp-tailed Grouse, 321
Sharp-tailed Sparrow, 351
Short-billed Dowitcher, 325
Short-billed Marsh Wren, 338
Short-eared Owl, 330
shrikes, 341
Shoveller, 315
Slate-colored Junco, 352
Smith Longspur, 353
Snow Bunting, 354
Snow Goose, 314

Snowy Egret, 311
Snowy Owl, 330
Snowy Plover, 323
Solitary Sandpiper, 324
Solitary Vireo, 341
Song Sparrow, 353
Sora, 322
Sparrow Hawk, 320
sparrows, 348-354
Spotted Sandpiper, 324
Sprague Pipit, 340
Starling, 341
Steller Jay, 336
Stilt Sandpiper, 325
Summer Tanager, 348
Surf Scoter, 317
Swainson Hawk, 319
swallows, 335-336
Swallow-tailed Kite, 318
Swamp Sparrow, 353
swans, 313
swift, 331
Sycamore Warbler, 344

tanagers, 348
Tennessee Warbler, 342
terns, 328
thrashers, 338
thrushes, 339-340
towhees, 350
Townsend Solitaire, 340
Townsend Warbler, 344
Tree Sparrow, 352
Tree Swallow, 335
Trumpeter Swan, 313
Tufted Titmouse, 337
Turkey, 321
Turkey Vulture, 317

Upland Plover, 324

Varied Thrush, 339
Veery, 339
Vesper Sparrow, 351
Violet-green Swallow, 335
vireos, 341-342
Virginia Rail, 322
Virginia Warbler, 343
vultures, 317-318

warblers, 342-346
Warbling Vireo, 342
Water Pipit, 340
Water-turkey, 311
waxwings, 340
Western Flycatcher, 334
Western Grebe, 310
Western Kingbird, 333
Western Meadowlark, 347
Western Sandpiper, 326
Western Tanager, 348
Western Wood Pewee, 335
Whip-poor-will, 331
Whistling Swan, 313
White-breasted Nuthatch, 337
White-crowned Sparrow, 353
White-eyed Vireo, 341
White-faced Glossy Ibis, 313
White-fronted Goose, 314
White-necked Raven, 336
White Pelican, 311
White-rumped Sandpiper, 325
White-throated Sparrow, 353
White-winged Crossbill, 350
White-winged Junco, 352
White-winged Scoter, 317
Whooping Crane, 321
Willet, 324
Williamson Sapsucker, 333
Wilson Phalarope, 326
Wilson Snipe, 324
Wilson Warbler, 346
Winter Wren, 337
Wood Duck, 315
Wood Ibis, 312
woodpeckers, 331-333
Wood Thrush, 339
Worm-eating Warbler, 342
wrens, 337-338
Wright Flycatcher, 334

Yellow-bellied Flycatcher, 334
Yellow-bellied Sapsucker, 332
Yellow-billed Cuckoo, 329
Yellow-breasted Chat, 346
Yellow-crowned Night Heron, 312
Yellow-headed Blackbird, 347
Yellow Rail, 322
Yellow-shafted Flicker, 331
Yellow-throat, 345
Yellow-throated Vireo, 341
Yellow Warbler, 343

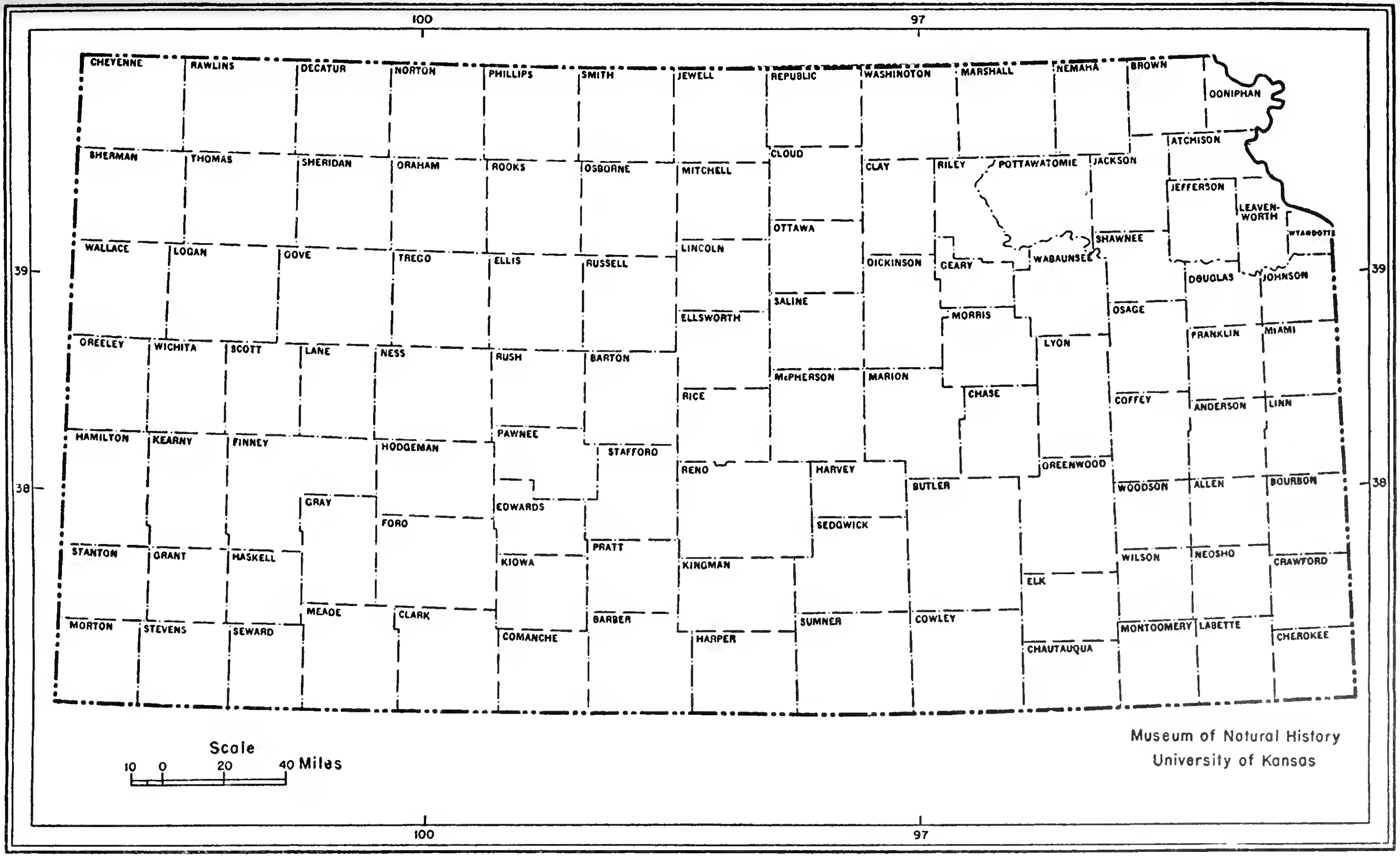

FIG. 1. Map of Kansas showing names of counties.

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25-9006

(Continued from inside of front cover)

14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15, 1951.
15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.
17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.
18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-317. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

***Vol. 6.** (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.

2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.

(Continued on back of cover)

(Continued from inside of back cover)

4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.

5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.

6. Distribution of some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.

7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.

8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.

9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.

10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.

11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.

12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.

13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.

14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.

15. Distribution and systematic position of the pigmy woodrat, Neotoma goldmani. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figs. in text. June 10, 1955.

Index. Pp. 625-651.

Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 2 pls., 26 figs. in text, 17 tables. September 1, 1954.

2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.

4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.

5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.

More numbers will appear in volume 8.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

More numbers will appear in volume 9.

University of Kansas Publications
Museum of Natural History

Volume 8, No. 6, pp. 361-416, 19 figures in text
April 2, 1956

A Population Study of the Prairie Vole (Microtus ochrogaster) in Northeastern Kansas

BY

EDWIN P. MARTIN

University of Kansas
Lawrence
1956

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Index. Pp. 605-638.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3.
*1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5.
1. Preliminary survey of a Paleocene faunule from the Angels Peak area, New Mexico. By Robert W. Wilson. Pp. 1-11, 1 figure in text. February 24, 1951.
2. Two new moles (Genus Scalopus) from Mexico and Texas. By Rollin H. Baker. Pp. 17-24. February 28, 1951.
3. Two new pocket gophers from Wyoming and Colorado. By E. Raymond Hall and H. Gordon Montague. Pp. 25-32. February 28, 1951.
4. Mammals obtained by Dr. Curt von Wedel from the barrier beach of Tamaulipas, Mexico. By E. Raymond Hall. Pp. 33-47, 1 figure in text. October 1, 1951.
5. Comments on the taxonomy and geographic distribution of some North American rabbits. By E. Raymond Hall and Keith R. Kelson. Pp. 49-58. October 1, 1951.
6. Two new subspecies of Thomomys bottae from New Mexico and Colorado. By Keith R. Kelson. Pp. 59-71, 1 figure in text. October 1, 1951.
7. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.
8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.
9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.
*10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202. 68 figures in text. December 15, 1951.
11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.
12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.
13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.

(Continued on inside of back cover)

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A POPULATION STUDY OF THE PRAIRIE VOLE (MICROTUS OCHROGASTER) IN NORTHEASTERN KANSAS

By

Edwin P. Martin

INTRODUCTION

Perhaps the most important species of mammal in the grasslands of Kansas and neighboring states is the prairie vole, *Microtus ochrogaster* (Wagner). Because of its abundance this vole exerts a profound influence on the quantity and composition of the vegetation by feeding, trampling and burrowing; also it is important in food chains which sustain many other mammals, reptiles and birds. Although the closely related meadow vole, *M. pennsylvanicus*, of the eastern United States, has been studied both extensively and intensively, relatively little information concerning *M. ochrogaster* has been accumulated heretofore.

I acknowledge my indebtedness to Dr. Henry S. Fitch, resident investigator on the University of Kansas Natural History Reservation. In addition to supplying guidance and encouragement in both the planning and execution of the investigation, Dr. Fitch made available for study the data from his extensive field work. Interest in and understanding of ecology were stimulated by his teaching and his example. Special debts are also acknowledged to Mr. John Poole for the use of his field notes and to Professor E. Raymond Hall, Chairman of the Department of Zoology, for several courtesies. Dr. R. L. McGregor of the Department of Botany at the University of Kansas assisted with the identification of some of the plants. Drawings of skulls were made by Victor Hogg.

Of the numerous publications concerning *Microtus pennsylvanicus,* those of Bailey (1924), Blair (1940; 1948) and Hamilton (1937a; 1937c; 1940; 1941) were especially useful in supplying background and suggesting methods for the present study. Publications not concerned primarily with voles, that were especially valuable to me in providing methods and interpretations applicable to my study, were those of Blair (1941), Hayne (1949a; 1949b), Mohr (1943; 1947), Stickel (1946; 1948) and Summerhayes (1941). Faunal and ecological reports dealing with *M. ochrogaster* and containing useful information on habits and habitat included those of Black (1937:200-202), Brumwell (1951:193-200; 213), Dice (1922:46) and Johnson (1926). Lantz (1907) discussed the economic relationships of *M. ochrogaster*; the section of his report concerning the effects of voles on vegetation was especially useful to me.

Fisher (1945) studied the voles of central Missouri and obtained information concerning food habits and nesting behavior. Jameson (1947) studied *M. ochrogaster* on and near the campus of the University of Kansas. His report is especially valuable in its treatment of the ectoparasites of voles. In my investigation I have concentrated on those aspects of the ecology of voles not treated at all by Fisher and Jameson, or mentioned but not adequately explored by them. Also I have attempted to obtain larger samples.

The University of Kansas Natural History Reservation, where almost all of the field work was done, is an area of 590 acres, comprising the northeasternmost part of Douglas County, Kansas. Situated in the broad ecotone between the deciduous forest and grassland, the reservation provides a variety of habitat types (Fitch, 1952). Before 1948, much of the area had been severely overgrazed and the original grassland vegetation had been largely replaced by weeds. Since 1948 there has been no grazing or cultivation. The grasses have partially recovered and, in the summer of 1952, some grasses of the prairie climax were present even on the parts of the Reservation which had been most heavily overgrazed. Illustrative of the changes on the Reservation were those observed in House Field by Henry S. Fitch (1953: *in litt.*). He recalled that in July, 1948, the field supported a closely grazed, grassy vegetation providing insufficient cover for *Microtus*, with such coarse weeds as *Vernonia*, *Verbena* and *Solanum* constituting a large part of the plant cover. By 1950, the same area supported a lush stand of grass, principally *Bromus inermis*, and supported many woody plants. Similar changes occurred in the other study areas on the Reservation. Although insufficient time has elapsed to permit analyses of successional changes, it seems that trees and shrubs are gradually encroaching on the grassland throughout the Reservation.

The vole population has changed radically since the Reservation was established. In September and October of 1948, when Fitch began his field work, he maintained lines of traps totaling more than 1000 trap nights near the future vole study plots without capturing a single vole. In November and December, 1948, he caught several voles near a small pond on the Reservation and found abundant sign in the same area. Late in 1949 he began to capture voles over the rest of the Reservation, but not until 1950 were voles present in sufficient numbers for convenient study.

I first visited the Reservation and searched there for sign of voles in the summer of 1949. I found hardly any sign. In the area around the pond mentioned above, however, several systems of runways were discovered. This area had been protected from grazing for several years prior to the reservation of the larger area. In House Field, where my main study plot was to be established, there was no sign of voles. Slightly more than a year later, in October, 1950, I began trapping and found *Microtus* to be abundant on House Field and present in smaller numbers throughout grassland areas of the Reservation.

GENERAL METHODS

The present study was based chiefly on live-trapping as a means of sampling a population of voles and tracing individual histories without eliminating the animals. Live-trapping disturbs the biota less than snap-trapping and gives a more reliable picture of the mammalian community (Blair, 1948:396; Cockrum, 1947; Stickel, 1946:158; 1948:161). The live-traps used were modeled after the trap described by Fitch (1950). Other types of traps were tested from time to time but this model proved superior in being easy to set, in not springing without a catch, in protecting the captured animal and in permitting easy removal of the animal from the trap. A wooden box was placed inside the metal shelter attached to each trap and, in winter, cotton batting or woolen scraps were placed inside the boxes for nesting material. With this insulation against the cold, voles could survive the night unharmed and could even deliver their litters successfully. In summer the nesting material was removed but the wooden box was retained as insulation against heat.

Bait used in live-traps was a mixture of cracked corn, milo and wheat, purchased at a local feed store. The importance of proper baiting, especially in winter, has been emphasized by Howard (1951) and Llewellyn (1950) who found an adequate supply of energy-laden food, such as corn, necessary in winter to enable small rodents to maintain body temperature during the hours of captivity. The rare instances of death of voles in traps in winter were associated with wet nesting material, as these animals can survive much lower temperatures when they are dry. Their susceptibility to wet and cold was especially evident in rainy weather in February and March.

Preventing mortality in traps was more difficult in summer than in winter. The traps were set in any available shade of tall grass or weeds; or when such shade was inadequate, vegetation was pulled and piled over the nest boxes. The traps usually were faced north so that the attached number-ten cans, which served as shelters, cast shadows over the hardware cloth runways during midday. Even these measures were inadequate when the temperature reached 90°F. or above. Such high temperatures rarely occurred early in the day, however, so that removal of the animals from traps between eight and ten a. m. almost eliminated mortality. Those individuals captured in the night were not yet harmed, but it was already hot enough to reduce the activity of the voles and prevent further captures until late afternoon. When it was necessary to run trap lines earlier, the traps were closed in the morning and reset in late afternoon.

Reactions of small mammals to live-traps and the effects of prebaiting were described by Chitty and Kempson (1949). In general, the results of my trapping program fit their conclusions. Each of my trapping periods, consisting of seven to ten consecutive days, showed a gradual increase in the number of captures per day for the first three days, with a tendency for the number of captures to level off during the remainder of the period. Leaving the traps baited and locked open for a day or two before a trapping period tended to increase the catch during the first few days of the period without any corresponding increase during the latter part of the period. Initial reluctance of the voles to enter the traps decreased as the traps became familiar parts of their environment.

At the beginning of the study the traps were set in a grid with intervals of 20 feet. The interval was increased to 30 feet after three months because a larger area could thus be covered and no loss in trapping efficiency was apparent. The traps were set within a three foot radius of the numbered stations, and were locked and left in position between trapping periods.

Each individual that was captured was weighed and sexed. The resulting data were recorded in a field notebook together with the location of the capture and other pertinent information. Newly captured voles were marked by toe-clipping as described by Fitch (1952:32). Information was transferred from the field notebook to a file which contained a separate card for each individual trapped.

In the course of the program of live-trapping, many marked voles were recaptured one or more times. Most frequently captured among the females were number 8 (33 captures in seven months) and number 73 (30 captures in eight months). Among the males, number 37 (21 captures in six months) and number 62 (21 captures in eight months) were most frequently taken. The mean number of captures per individual was 3.6. For females, the mean number of captures per individual was 3.8 and for males it was 3.4. Females seemingly acquired the habit of entering traps more readily than did males. No correlation between any seasonally variable factor and the number of captures per individual was apparent. To a large degree, the formation of trap habits by voles was an individual peculiarity.

In order to study the extent of utilization of various habitats by *Microtus*, a number of areas were sampled with Museum Special snap-traps. These traps were set in linear series approximately 25 feet apart. The number of traps used varied with the size of the area sampled and ranged from 20 to 75. The lines were maintained for three nights. The catch was assumed to indicate the relative abundance of *Microtus* and certain other small mammals but no attempt to estimate actual population densities from snap-trapping data was made. In August, 1952, when the live-trapping program was concluded, the study areas were trapped out. The efficiency of the live-trapping procedure was emphasized by the absence of unmarked individuals among the 45 voles caught at that time.

Further details of the methods and procedures used are described in the appropriate sections which follow.

HABITAT

Although other species of the genus *Microtus*, especially *M. pennsylvanicus*, have been studied intensively in regard to habitat preference (Blair, 1940:149; 1948:404-405; Bole, 1939:69; Eadie, 1953; Gunderson, 1950:32-37; Hamilton, 1940:425-426; Hatt, 1930:521-526; Townsend, 1935:96-101) little has been reported concerning the habitat preferences of *M. ochrogaster*. Black (1937: 200) reported that, in Kansas, *Microtus* (mostly *M. ochrogaster*) preferred damp situations. *M. ochrogaster* was studied in western Kansas by Brown (1946:453) and Wooster (1935:352; 1936:396) and found to be almost restricted to the little-bluestem association of the mixed prairie (Albertson, 1937: 522). Brumwell (1951:213), in a survey of the Fort Leavenworth Military Reservation, found that *M. ochrogaster* preferred sedge and bluegrass meadows but occurred also in a sedge-willow association. Dice (1922:46) concluded that the presence of green herbage, roots or tubers for use as a water source throughout the year was a necessity for *M. ochrogaster*. Goodpastor and Hoffmeister (1952:370) found *M. ochrogaster* to be abundant in a damp meadow of a lake margin in Tennessee. In a study made on and near the campus of the University of Kansas, within a few miles of the area concerned in the present report, Jameson (1947:132) found that voles used grassy areas in spring and summer, but that in the autumn, when the grass began to dry, they moved to clumps of Japanese honeysuckle (*Lonicera japonica*) and stayed among the shrubbery throughout the winter. Johnson (1926:267, 270) found *M. ochrogaster* only in uncultivated areas where long grass furnished adequate cover. He stated that the entire biotic association, rather than any single factor, was the key to the distribution of the voles. None of these reports described an intensive study of the habitat of voles, but the data presented indicate that voles are characteristic of grassland and that *M. ochrogaster* can occupy drier areas than those used by *M. pennsylvanicus.* Otherwise, the preferred habitats of the two species seem to be much the same.

In the investigation described here I attempted to evaluate various types of habitats on the basis of their carrying capacity at different stages of the annual cycle and in different years. The habitats were studied and described in terms of yield, cover and species composition. The areas upon which live-trapping was done were studied most intensively.

These two areas, herein designated as House Field and Quarry Field, were both occupied by voles throughout the period of study. Population density varied considerably, however (Fig. 5). Both of these areas were dominated by *Bromus inermis,* and, in clipped samples taken in June, 1951, this grass constituted 67 per cent of the vegetation on House Field and 54 per cent of the vegetation on Quarry Field. Estimates made at other times in 1950, 1951 and 1952 always confirmed the dominance of smooth brome and approximated the above percentages. Parts of House Field had nearly pure stands of this grass. Those traps set in spots where there was little vegetation other than the dominant grass caught fewer voles than traps set in spots with a more varied cover. *Poa pratensis* formed an understory over most of the area studied, especially on House Field, and attained local dominance in shaded spots on both fields. The higher basal cover provided by the *Poa* understory seemed to support a vole population larger than those that occurred in areas lacking the bluegrass. Disturbed situations, such as roadsides, were characterized by the dominance of *Bromus japonicus.* This grass occurred also in low densities over much of the study area among *B. inermis.* Other grasses present included *Triodia flava,* common in House Field, but with only spotty distribution in Quarry Field; *Elymus canadensis,* distributed over both areas in spotty fashion and almost always showing evidence of use by voles and other small mammals; *Aristida oligantha* and *Bouteloua curtipendula,* both more common on the higher and drier Quarry Field; *Panicum virgatum, Setaria* spp., especially on disturbed areas; and three bluestems, *Andropogon gerardi, A. virginicus* and *A. scoparius.* The bluestems increased noticeably during the study period (even though grasses in general were being replaced by woody plants) and they furnished a preferred habitat for voles because of their high yield of edible foliage and relatively heavy debris which provided shelter.

On House Field the most common forbs were *Vernonia baldwini, Verbena stricta* and *Solanum carolinense.* On Quarry Field, *Solidago* spp. and *Asclepias* spp. were also abundant. All of them seemed to be used by the voles for food during the early stages of growth, when they were tender and succulent. The fruits of the horse nettle (*Solanum carolinense*) were also eaten. The forbs themselves did not provide cover dense enough to constitute good vole habitat. Mixed in a grass dominated association they nevertheless raised the carrying capacity above that of a pure stand of grass. Other forbs noted often enough to be considered common on both House Field and Quarry Field included *Carex gravida,* observed frequently in House Field and less often in Quarry Field; *Amorpha canescens,* more common in Quarry Field; *Tradescantia bracteata, Capsella bursapastoris, Oxalis violacea, Euphorbia marginata, Convolvulus arvensis, Lithospermum arvense, Teucrium canadense, Physalis longifolia, Phytolacca americana, Plantago major, Ambrosia trifida, A. artemisiifolia, Helianthus annuus, Cirsium altissimum* and *Taraxacum erythrospermum.* Both areas were being invaded from one side by forest-edge vegetation; the woody plants noted included *Prunus americana, Rubus argutus, Rosa setigera, Cornus drummondi, Symphoricarpus orbiculatus, Populus deltoides* and *Gleditsia triacanthos.*

In House Field the herbaceous vegetation was much more lush than in Quarry Field and woody plants and weeds were more abundant. A graveled and heavily used road along one edge of House Field, leading to the Reservation Headquarters, was a barrier which voles rarely crossed. A little-used dirt road crossing the trapping plot in Quarry Field constituted a less effective barrier. The disturbed areas bordering the roads were likewise little used and tended to reinforce the effects of the roads as barriers. There were almost pure stands of *Bromus japonicus* along both roads. No mammal of any kind was taken in traps set where this grass was dominant.

Because seasonal changes in vole density followed the curve for rate of growth of the complex of grasses on the Reservation, and because years in which there was a sparse growth of plants due to dry weather showed a decrease in the density of voles, the relationships between productivity of plants and vole population levels on the two study areas were investigated. In both fields the composition of the plant cover was similar, and the differences were chiefly quantitative. In June, 1951, ten square-meter quadrats were clipped on each of the areas to be studied. The clippings from each were dried in the sun and weighed. From Quarry Field the mean yield amounted to 1513 ± 302 lbs. per acre; while from House Field the yield was 2351 ± 190 lbs. per acre (Table 1). Using experience gained in making these samples, I periodically estimated the relative productivity of the two areas. House Field was from 1.5 to 3 times as productive as Quarry Field during the growing seasons of 1951 and 1952. Although House Field, being more productive, usually supported a larger population of voles than Quarry Field the reverse was true at the time of the clipping (Fig. 5).

Although no explanation was discovered which accounted fully for the seeming aberration, two sets of observations were made that may bear on the problem. In June, 1951, the population of voles and cotton rats on Quarry Field was increasing rapidly whereas in House Field that trend was reversed. The trends were reflected by the percentages of immature individuals in the two populations and by the ratios of the June, 1951, densities to the March, 1951, densities (Table 1). Perhaps the density curve was determined in part by factors inherent in the population and, to that extent, was fluctuating independently of the environment (Errington, 1946:153).

The flood in 1951 reduced the population of voles and obscured the normal seasonal trends. Although House Field produced a heavier crop of vegetation, Quarry Field produced a larger crop of rodents, chiefly *Microtus* and *Sigmodon.* In House Field, however, the ratio of *Sigmodon* to *Microtus* was notably higher. Presumably the cotton rats competed with the voles and exerted a depressing effect on their numbers. The intensity of the effect seemed to depend on the abundance of both species. That this depressing effect involved more than direct competition for plant food was suggested by the fact that in House Field, with a heavy crop of vegetation and a seemingly high carrying capacity for both herbivorous rodents, the biomass of voles, and of all rodents combined, were lower than in Quarry Field which had less vegetation and fewer cotton rats. The relationships between voles and cotton rats are discussed further later in this report.

TABLE 1. RELATIONSHIP BETWEEN YIELD AND VARIOUS POPULATION DATA

	House Field	Quarry Field
Yield in June, 1951, lbs./acre	2351 ± 190	1513 ± 302
Microtus, June, 1951, gms./acre	3867	5275
Per cent immature *Microtus*, June, 1951	29.85	38.02
Ratio *Microtus*, June/March	0.73	2.63
Sigmodon, June, 1951, gms./acre	1376	746
Per cent immature *Sigmodon*, June, 1951	35.72	44.44
Ratio *Sigmodon*, June/March	1.40	2.25
Microtus-Sigmodon, June, 1951, gms./acre	5243	6021
Microtus mean, gms./acre/month	2922	1831
Sigmodon mean, gms./acre/month	802	335
Sigmodon-Microtus, gms./acre/month	3728	2166

When the centers of activity (Hayne, 1949b) of individual voles were plotted it was seen that there was a shift in the places of high density of voles on the trapping areas. This shift seemed to be related to the advance of the forest edge with such woody plants as *Rhus* and *Symphoricarpos* and young trees invading the area. These shifts were clearly shown when the distribution of activity centers on both areas in June, 1951, was compared with the distribution in June, 1952 (Fig. 1). The shift was gradual and the more or less steady progress could be observed by comparing the monthly trapping records. It was perhaps significant that during the summers the centers of activity were less concentrated than during the winter. The shift of voles away from the woods was more nearly evident in winter when the voles were driven into areas of denser ground cover, which provided better shelter.

From 1948 to 1950 and again in 1952 and 1953 I trapped in various habitat types in a mixed prairie near Hays, Kansas. Before the great drought of the thirties, *Microtus ochrogaster* was the most common species of small mammal in that area. Since 1948, at least, it has been taken only rarely and from a few habitats. No voles have been taken from grazed sites. In a relict area, voles were trapped in a lowland association dominated by big bluestem. Since 1948 only one vole has been trapped in the more extensive hillside association characterized by a mixture of big bluestem, little bluestem and side-oats grama. None was taken in the upland parts of the relict area where buffalo grass and blue grama dominated the association.

In the pastured areas there are nine livestock exclosures established by the Department of Botany of Ft. Hays Kansas State College. These exclosures included many types of habitat found in the mixed prairie. All of these exclosures were trapped and voles were taken in only two of them. An exclosure situated near a pond, on low ground producing a luxuriant growth of big bluestem and western wheat grass, has supported voles in 1948, 1949, 1952 and 1953. An upland exclosure containing only short grasses also supported a few voles in 1953.

An examination of the nature of the various plant associations of the mixed prairie indicates that yield of grasses, amount of debris and basal cover may be critical factors in the distribution of voles. The association to which the voles seemed to belong was the lowland association. Hopkins *et al* (1952:401; 409) reported the yield of grasses from the lowland to be approximately twice as great as from the hillside and upland in most years. Probably equally important to the voles was the fact that debris accumulation in the lowland was

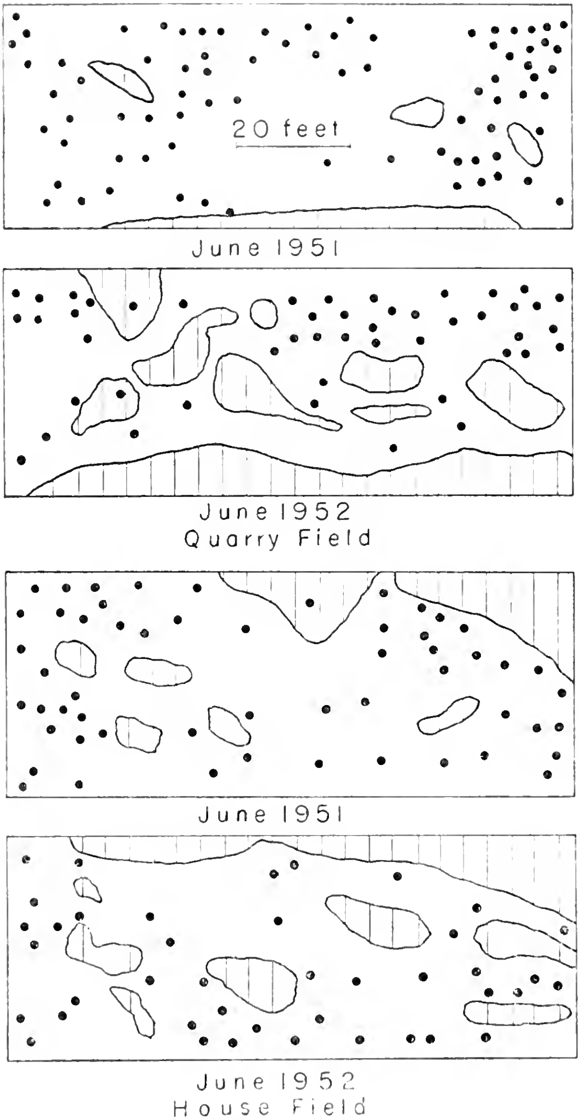


FIG. 1. Progressive encroachment of woody vegetation onto study areas, and the accompanying shift of the centers of populations of voles. Activity centers of individuals were calculated as described by Hayne (1949b) and are indicated by dots. The cross-hatched areas show places where the vegetation was influenced by the shade of woody plants.

approximately five times as great as in the upland and approximately 2.5 times as great as on the hillside (Hopkins, unpublished data). The unexpected presence of voles in the short grass exclosure was probably due to two factors. In ungrazed short grass, basal cover may reach 90 per cent (Albertson, 1937: 545), thus providing excellent cover for voles. Also, the ungrazed exclosure had greater yield and a thicker mat of debris than the grazed short grass surrounding it and was thus a relatively good habitat, although it did not compare favorably with the lowland type.

Samples of the populations of various areas, obtained by snap-trapping, gave further information regarding the types of vegetation preferred by voles. Voles were taken in all ungrazed and unmown grasslands trapped in eastern Kansas, although some of the areas were not used at all seasons of the year nor in years having a low population of *Microtus*. Reithro Field, similar to Quarry Field in its general aspect, had a heavy population of voles in the spring and summer of 1951, a time when voles were generally abundant. On the same area the population of small mammals was sampled in the summer of 1949 and, though occasional sign of voles was seen, not one vole was trapped. Later trapping, in the spring and summer of 1952, also failed to catch any voles and Fitch (1953, *in litt.*) caught none in several trapping attempts in 1953. These later times were characterized by a general scarcity of voles. Reithro Field was drier, with less dense vegetation, than the two main study areas and had larger percentages of little bluestem (*Andropogon scoparius*) and side-oats grama (*Bouteloua curtipendula*) and smaller percentages of *Vernonia, Verbena, Solanum* and *Solidago*.

Various species of foxtail (*Setaria*) dominated most roadsides in the vicinity of the Reservation. Voles almost always used these strips of grass but never were abundant in them. Voles were taken near the margin of a weedy field, fallow since 1948, but there was none in the middle of the field. Most individuals were confined to the grassy areas around the field and made only occasional forays away from the edge. The dam of a small pond on the Reservation and low ground near the water were used by *Microtus* at all times. In the summer of 1949 no voles were taken anywhere on the Reservation but their runways were more abundant around the pond than in the other places examined. Of all the areas studied in the summer of 1949, only the pond area had been protected from grazing in previous years. *Polygonum coccineum* was the most prominent plant in the pond edge association. A few voles were trapped in large openings in the woods, where a prairie vegetation remained and where voles seemingly lived in nearly isolated groups.

Voles were rarely taken in grazed or mown grassland or in fields of alfalfa, stubble or row crops. The critical factor in these cases seemed to be the absence of debris or other ground cover under which runways and nests could be concealed satisfactorily. Woods, rocky outcroppings and bare ground were not used regularly by voles. Fitch (1953, *in litt.*) has taken several *Microtus* in reptile traps set along a rocky ledge in woods but most of these voles were subadult males and seemed to be transients. Fields in the early stages of succession also failed to support a population of voles. Such areas on the Reservation were characterized by giant ragweed, horse weed, thistles and other coarse weeds. Basal cover was low and debris scanty. Not until an understory of grasses was established did a population of voles appear on such areas. The coarse weeds seemed to provide neither food nor cover adequate for the needs of the voles.

An analysis of trapping success at each station in House Field further clarified habitat preferences. The tendency of voles to avoid woody vegetation was again demonstrated. Not only was the population concentrated on that part of the study plot farthest from the forest edge but, as a general rule, voles tended to avoid single trees or clumps of shrubby plants wherever these occurred on the area. As an example, trap number 18 never caught more than one per cent of the monthly catch and in many trapping periods caught nothing. This trap was under a wild plum tree. Adjacent traps often were entered; the general area was the most heavily populated part of the study plot. Only under the plum tree was there a relatively unused portion.

Traps number 29 and 30, in the shade of a large honey locust tree, also caught but few voles. Trap number 30 was only six feet from the base of the tree and caught but one vole throughout the study period. These two traps caught more *Peromyscus leucopus* than any other pair, however, and both of them also caught pine voles (*M. pinetorum*). The area shaded by this tree permitted an extension of parts of the forest edge fauna into the grassland.

In spite of the marked general tendency to avoid woody plants, some voles made their runways around the roots of blackberry bushes, sumac and wild plum trees. Some nests were found under larger roots, as if placed there for protection. More vegetation was found under the woody plants which the voles chose to use for shelter than under those which they avoided. It seemed probable that the actual condition avoided by voles was the bareness of the ground (a result of the shade cast by the woody plants) rather than the woody plants themselves.

Running diagonally across the eastern half of the trapping plot in House Field there was a terracelike ridge of soil. On each side of this ridge there was a slight depression. Observations of the study plot in the growing season showed this strip to produce the most luxuriant vegetation of any part of the plot. Clip-quadrat studies confirmed this observation and showed the bluegrass understory to be especially heavy. This strip included the areas trapped by traps numbered 4, 5, 17, 18, 22, 23 and 37. With the exception of trap number 18, discussed above, these traps consistently made more captures than traps set in other parts of the plot. In winter, these traps also caught more harvest mice (*Reithrodontomys megalotis*) than any other comparable group of traps.

Although the amount of growing tissue of plants probably is at least as important to voles as the total amount of vegetation, some correlation seemed to exist between the density of grassy vegetation and the density of populations of voles. A mixed stand of grasses, with an obvious weedy component, can support a larger population of voles than can either a nearly pure stand of grass or the typical early seral stages dominated by weeds. Probably the more or less continual supply of young plants provided preferred food easily available to voles. A more homogenous vegetation would tend to pass through the young and tender stage as a unit, thus causing a feast to be followed by a relative famine.

POPULATION STRUCTURE

During the period of study the percentage of males in most of my samples was less than 50 per cent (Fig. 2). Only once, in June, 1952, did the mean percentage of males in samples from three areas (House Field, Quarry Field, Fitch traps) exceed that level and then it was only 50.1 per cent. On several occasions, however, the percentage of males in a sample from a single area was slightly above 50 per cent. The highest percentage of males recorded was 56.69 per cent, in a sample taken from the Quarry Field population in June, 1952. In the samples taken in April, 1952, the mean percentage of males was 39.67 per cent, the lowest mean recorded. The low point for one sample was 28.02 per cent in August, 1952, from Quarry Field. The mean percentage of males in all samples taken was 45.02 ± 2.72 per cent. Percentages observed would occur in random samples taken from a population with 50 per cent males less than one per cent of the time. Exactly 50 per cent of the young in the 65 litters examined were classified as males but the sample was small and the sexing of newborn individuals was difficult.

The extent to which sex ratios in samples were affected by trapping procedure was not determined. A possibility considered was that the greater wandering tendency of males (Blair, 1940:154; Hamilton, 1937c:261; Townsend, 1935:98) impaired the formation of trap habits (Chitty and Kempson, 1949:536) on their part and thus unbalanced the sex ratios of the samples. If this were the explanation, the apparent sex ratio on larger areas would more nearly approximate the true ratio, and the frequency of capture of females would exceed that of males. The evidence is somewhat equivocal. In the populations described here the mean number of captures per individual per month was 2.31 for females, which was significantly greater (at the one per cent level) than the 2.20 captures per individual per month which was the mean number for males. This difference supports the idea that differences in habits between the sexes result in distorted sex ratios in samples obtained by live-trapping. Mean percentages of males did not, however, differ significantly between the House Field-Quarry Field samples and the samples from the Fitch trapping area, nearly five times as large.

Three age classes, juvenal, subadult and adult, were separated on the basis of condition of pelage. The percentage of adults in populations varied seasonally (Fig. 2). January, February and March were the months when the adult fraction of the population was highest and October and November were low points, with May and June showing percentages almost as low. The only marked variation in this seasonal pattern occurred in July and August, 1952, when the percentage of adults rose sharply. This was due to a depression in the reproductive rate during the dry summer of 1952, which is discussed later in this report. Juveniles made up only a small fraction of the population from December through March and a relatively large fraction in the October-November and May-June periods (Fig. 2). Again, July and August of 1952 were exceptions to the pattern as the percentages of juveniles in these months fell to midwinter levels. As expected, the curve of the percentages of subadults in the population followed that of the juveniles and preceded that of the adults. The mean percentages for the thirty month period for which data were available were: adults, 77.72±4.48 per cent; subadults, 14.06±3.14 per cent; and juveniles, 8.22±2.62 per cent. Seasonal and yearly changes in the population structure occurred, with notable variation in the ratio of breeding females to the entire population, as discussed in this report under the heading of reproduction.

Since some of the juveniles did not move enough to be readily trapped, the real percentage of juveniles in the population was probably far greater than

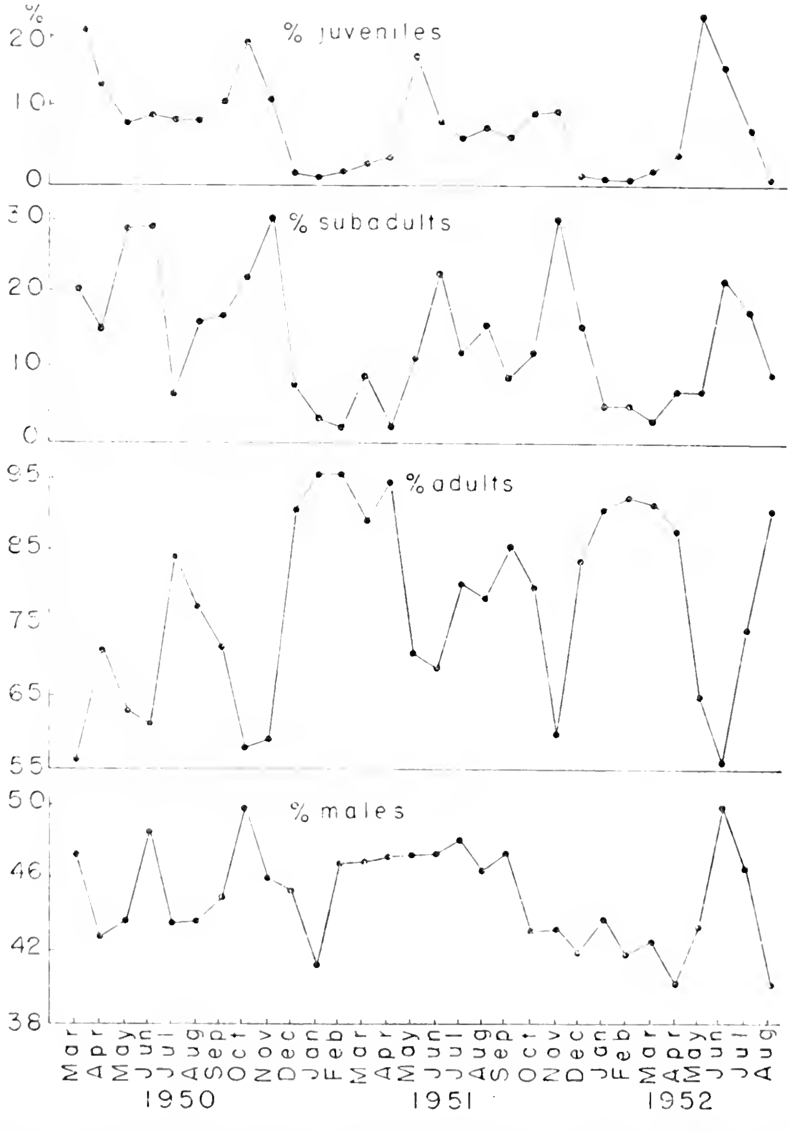


FIG. 2. Graphs of population structure showing the monthly changes in the mean percentages of juveniles, subadults, adults and males in samples from the three study areas.

that shown by trapping data. I tried, therefore, to estimate the number of juveniles on the study plot each month by multiplying the number of lactating females by the mean litter size. As expected, the results were consistently higher than the estimate based on trapping data. The discrepancy was largest in April, May, June and October. During the winter there was no important difference between the two estimates. Even when the discrepancy was greatest, the estimated weight of the juveniles missed by trapping was not large enough to modify the picture of habitat utilization in any important way. I chose, therefore, to count only those juveniles actually trapped. Although probably consistently too low, such a figure seemed more reliable than an estimate made on any other basis.

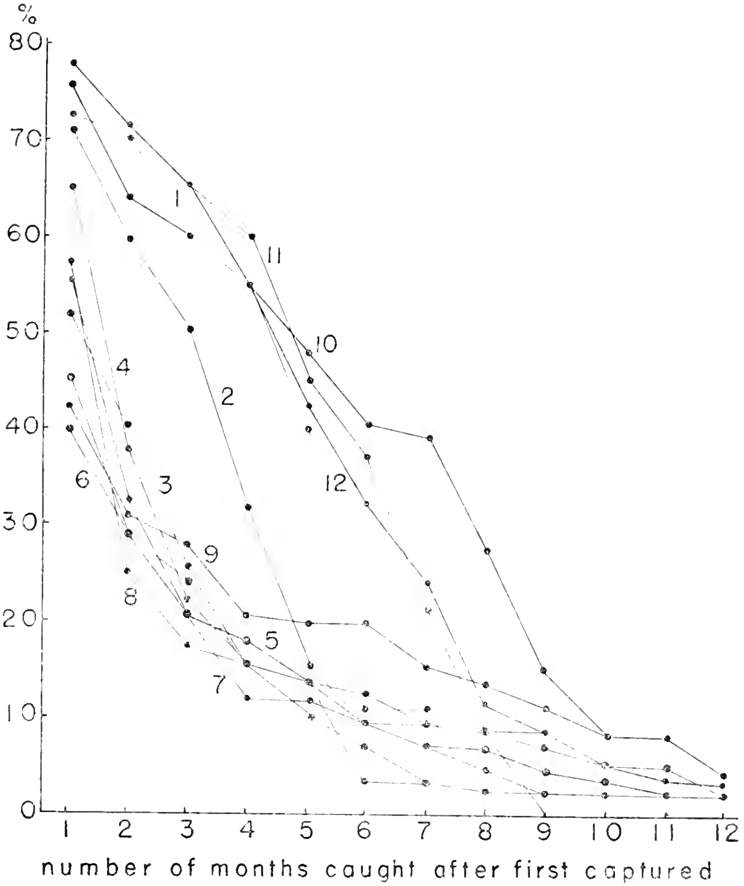


FIG. 3. Percentages of individuals captured each month surviving in subsequent months. The graph shows differential survival according to time of birth. Individuals born in autumn seem to have a longer life expectancy. The numbers on the lines refer to months of first capture.

A study of the age groups in each month's population revealed a differential survival based on the season of birth. Blair (1948:405) found that chances of survival in *Microtus pennsylvanicus* were approximately equal throughout the year. In the present populations of *M. ochrogaster,* however, voles born in October, November, December and January tended to live longer than those born in other months (Fig. 3). Presumably these animals, born in autumn and early winter, were more vigorous than their older competitors and were therefore better able to survive the shrinking habitat of winter. Their continued survival after large numbers of younger voles had been added to the population probably was permitted by the expanding habitat of spring and summer. The percentage of the population surviving the winter of 1951-1952 was approximately double the percentage surviving the winter of 1950-1951. This difference seemed to be due to the smaller population entering the winter of 1951-1952 rather than any major difference in the environmental resistance.

As a consequence of the differential survival, most of the breeding population in the spring was made up of animals born the previous October and November. Fig. 4 shows that in February, when the percentage of breeding females ordinarily began to rise, 51.6 per cent of the population was born in the previous October and November. Voles born in these two months continued to form a large part of the population through March (45.1 per cent), April (38.5 per cent), May (23.9 per cent), June (18.7 per cent) and July (16.2 per cent) (Fig. 4). These percentages suggest that the habitat conditions in October and November were probably important in determining the population level for at least the first half of the next year.

POPULATION DENSITY

Population densities were ascertained on the study areas by means of the live-trapping program. Blair (1948:396) stated that almost all small mammals old enough to leave the nest (except shrews and moles) are captured by live-trapping. My experience, and that of other workers on the Reservation, requires modification of such a statement. The distance between traps is an important factor in determining the efficiency of live-trapping. As mentioned earlier, when House Field and Quarry Field were trapped out at the conclusion of the live-trapping program no unmarked voles were taken. This showed that the 30 foot interval between traps was short enough to cover the area as far as *Microtus* was concerned. The fact that unmarked adults were caught almost entirely in marginal traps is additional evidence. On the other hand, the Fitch traps were 50 feet apart and voles seemed to have lived within the grid for several months before being captured. Fitch (1954:39) has shown that some kinds of small mammals are missed in a live-trapping program because of variation in bait acceptance, both seasonal and specific.

A few individuals, missed in a trapping period, were captured again in subsequent months. These voles were assumed to have been present during the month in which they were not caught. The area actually trapped each month was estimated by a modification of the method proposed by Stickel (1946:153). The average maximum move was calculated each month and a strip one half the average maximum move in width was added to each side of the study area actually covered by traps. The study plots were bounded in part by gravel roads and forest edge acting as barriers, and for these parts no marginal strip was added. Trap lines on the opposite sides of these roads rarely caught marked voles that had crossed in either direction. It is perhaps advisable to say here that the size of House Field and Quarry Field study plots (0.56 acres)

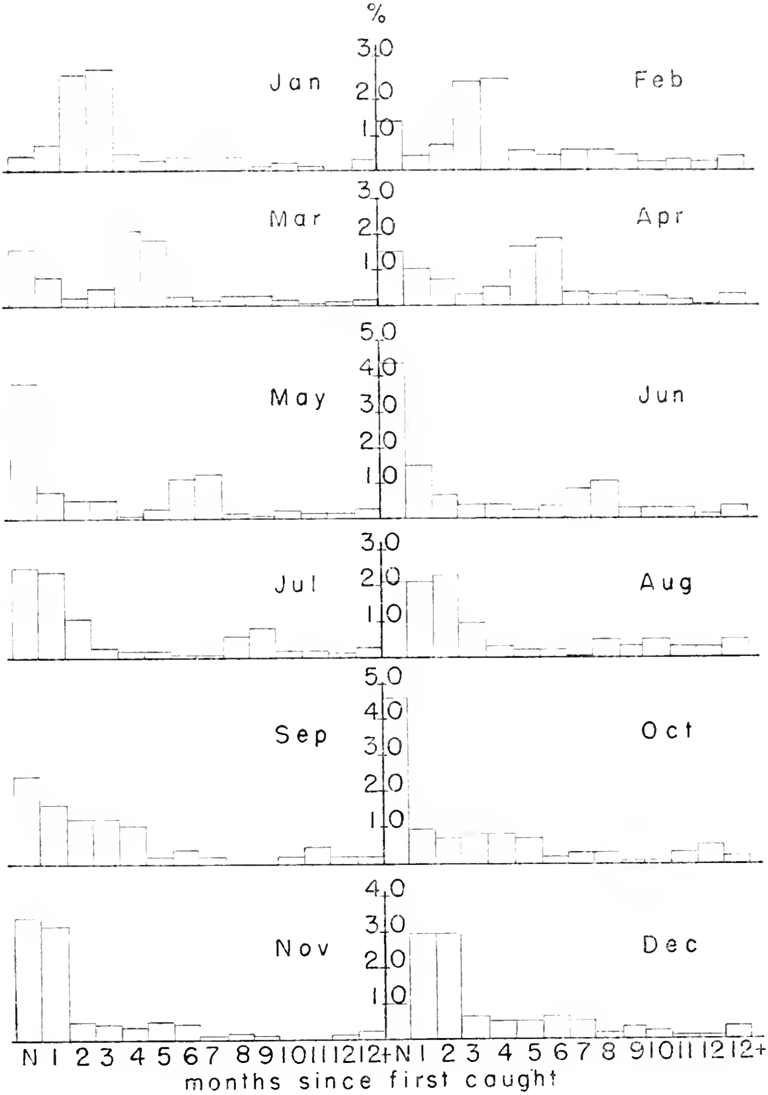


FIG. 4. Differential survival of voles according to month when first caught. Each column represents the percentage of the monthly sample first caught in each of the preceding months. Those voles caught first in October and November survived longer than those first caught in other months. Relatively few individuals remained in the population as long as one year.

was too small for best results in estimating population levels (Blair, 1941:149). In the computations of population levels the data for males and females were combined, because no significant difference between the average maximum move of the sexes was apparent.

Fluctuations of the populations were graphed in terms of individuals per acre (Fig. 5). The variation was great in the 30 month period for which data were available, and was both chronological and topographical. The lowest density recorded was 25.2 individuals per acre and the highest density was 145.8 individuals per acre. The weight varied from a low of 847 grams per acre to a high of 5275 grams per acre.

There are few records of density of *M. ochrogaster* in the literature. Brumwell (1951:213) found nine individuals per acre in a prairie on the Fort Leavenworth Military Reservation and Wooster (1939:515) reported 38.5 individuals per acre for *M. o. haydeni* in a mixed prairie in west-central Kansas. High densities for *M. pennsylvanicus* reported in the literature include 29.8 individuals per acre (Blair, 1948:404), 118 individuals per acre (Bole, 1939:69), 160-230 individuals per acre (Hamilton, 1937b:781) and 67 individuals per acre (Townsend, 1935:97).

Because the study period included one period of unusually high rainfall and one year of unusually low rainfall, the normal pattern of seasonal variation of population density was obscured. An examination of the data suggested, however, that the greatest densities were reached in October and November with a second high point in the April-May-June period. These high points generally followed the periods of high levels of breeding activity (Fig. 8). The autumn rise in population may have been due, in part, to the addition of spring and early summer litters to the breeding population, but the rise occurred too late in the year to be explained by that alone. Another factor may have been the spurt in growth of grasses occurring in Kansas in early autumn, in September and October. There was a seeming correlation between high rainfall with rapid growth of grasses and reproductive activity, and, secondarily with high population densities of voles. These relationships are discussed in connection with reproduction. Lowest annual densities were found to occur in January when there is but little breeding activity and when rainfall is low and plant growth has ceased.

Marked deviation from the usual seasonal trends accompanied flood and drought. In the flood of July, 1951, although the study areas were not inundated, the ground was saturated to the extent that every footprint at once became a puddle. Immediately after the floods, on all three areas studied, populations were found to have been drastically reduced. The effect was most severe on the population of House Field, the lowest area studied, and the recovery of the population there was much slower than that of those on the other study areas (Fig. 5). Newborn voles were killed by the saturated condition of the ground in which they lay. The more precocious young of *Sigmodon hispidus* survived wetting better. They thus acquired an advantage in the competitive relationship between cotton rats and voles. These relationships are discussed more fully in the section on mammalian associates of *Microtus*.

Adverse effects of heavy rainfall on populations of small mammals have been reported by Blair (1939) and others. Goodpastor and Hoffmeister (1952:

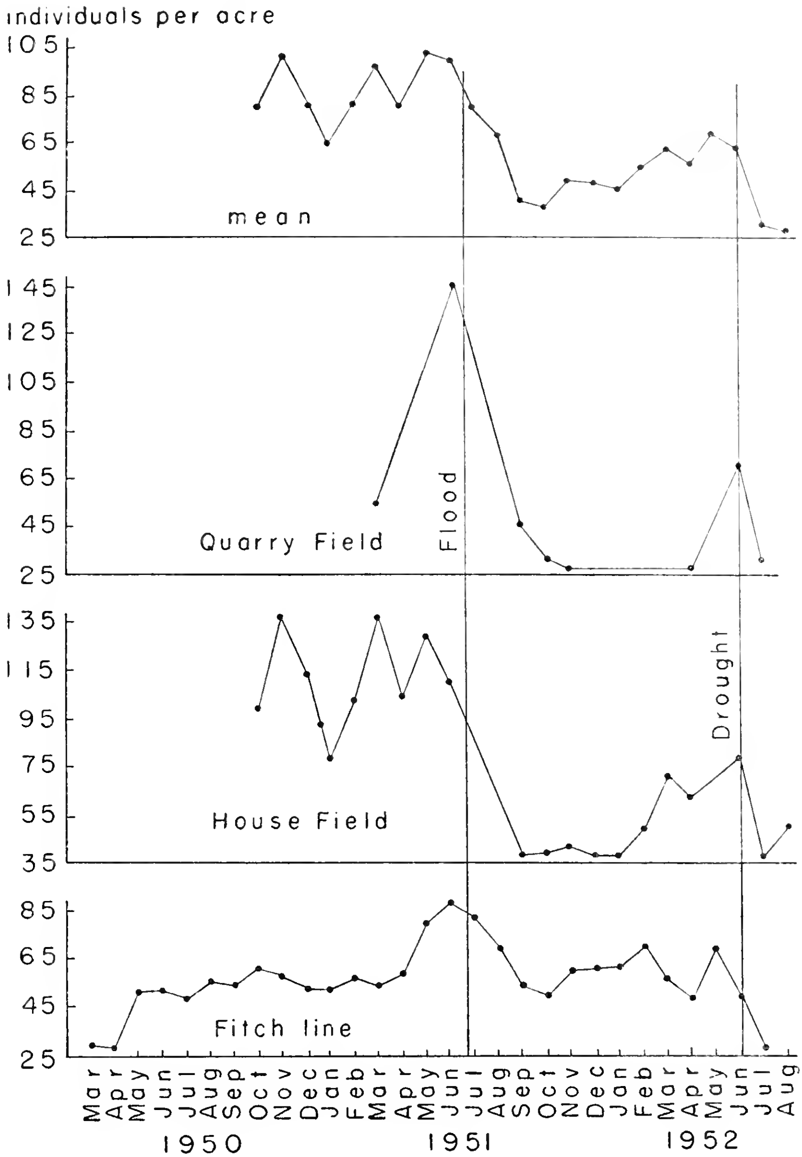


FIG. 5. Variations in density of voles from three populations, as shown by live-trapping, and the mean density of these populations. Juveniles are not represented in their true numbers since many voles were caught first as subadults. The samples from the Fitch trap line were incomplete due to the wide spacing of the traps.

370) reported that inundation sharply reduced populations of *M. ochrogaster* for a year after flooding but that the area was then reoccupied by a large population of voles. Such a reoccupation may have begun on the areas of this study in the spring of 1952 when the upward trend of the population was abruptly reversed by drought. While cotton rats were abundant their competition may have been an important factor in depressing population levels of voles. The population of voles began to rise only after the population of cotton rats had decreased (Fig. 19).

In the unusually dry summer of 1952, there was a marked decline of population levels beginning in June and continuing to August when my field work was terminated. Dr. Fitch (1953, *in litt.*) informed me that the decline continued through the winter of 1952-53 and into the summer of 1953, until daily catches of *Microtus* on the Reservation were reduced to 2-10 per cent of the number caught on the same trap lines in the summer of 1951. The drought seemed to affect population levels by inhibiting reproduction, as described elsewhere in this report. A similar sensitivity to drought was reported by Wooster (1935:352) who found *M. o. haydeni* decreased more than any other species of small mammal after the great drought of the thirties.

No evidence of cycles in *M. ochrogaster* was observed in this investigation. All of the fluctuations noted were adequately explained as resulting from the direct effects of weather or from its indirect effect in determining the kinds and amounts of vegetation available as food and shelter.

The differences in densities supported by the various habitats were discussed earlier in connection with the analysis of habitats.

HOME RANGE

Home ranges were calculated for individual voles according to the method described by Blair (1940:149-150). The term, home range, is used as defined by Burt (1943:350-351). Only those voles captured at least four times were used for the home range studies. Individuals which included the edge of the trap grid in their range were excluded unless a barrier existed (see description of habitat) confining the seeming range to the study area.

The validity of home range calculations has been challenged (Hayne, 1950:39) and special methods of determining home range have been advocated by a number of authors. The ranges calculated in this study are assumed to approximate the actual areas used by individuals and are considered useful for comparison with other ranges calculated by similar methods, but no claim to exactness is intended. It is obvious, for instance, that many plotted ranges contain so-called blank areas which, at times, are not actually used by any vole (Elton, 1949:8; Mohr, 1943:553). Studies of the movements of mammals on a more detailed scale, perhaps by live-traps set at shorter intervals and moved frequently, are needed to increase our understanding of home range.

In order to test the reliability of the range calculated, an examination of the relationship between the size of the seeming range and the number of captures was made. For the first three months, trapping on House Field was done with a 20 foot grid and throughout the remainder of the study a 30 foot grid was used. The effect of these different spacings on the size of the seeming home range was also investigated. Hayne (1950:38) found that an increase in the distance between traps caused an increase in the size of the seeming home range, but in my study the increased interval between traps was not accompanied by any change in the sizes of the calculated ranges.

The number of captures, above the minimum of four, did not seem to be a factor in determining the size of the calculated monthly range. A seeming relationship was observed between the number of times an individual was trapped and the total area used during the entire time the vole was trapped. Closer examination revealed that the most important factor was the length of time over which the vole's captures extended. Table 2 shows the progressive increase in sizes of the mean range of animals taken over periods of time from one month to ten months.

TABLE 2. RELATIONSHIP BETWEEN HOME RANGE SIZE AND LENGTH OF TIME ON THE STUDY AREA

No. months on area	1	2	3	4	5	6	7	8	9	10
Mean range in acres	.09	.09	.10	.14	.13	.17	.22	.22	.26	.24

Nothing concerning the home range of *Microtus ochrogaster* was found in the literature. Several workers, including Blair (1940) and Hamilton (1937c), have studied the home range of *M. pennsylvanicus.* Blair (1940:153) reported a larger range for males than for females in all habitats and in all seasons represented in his sample. In *M. ochrogaster,* however, I found that the mean monthly range for both sexes was 0.09 of an acre. Blair (*loc. cit.*) reported no individuals with a range so small as that mean, but Hamilton (*op. cit.*:261) mentioned two voles with ranges of less than 1200 square feet. The mean total range used by an individual during the entire time it was being trapped showed a slight difference between the sexes. Males used an average of 0.14 of an acre whereas females used an average of but 0.12 of an acre. This suggested that, as in *M. pennsylvanicus* (Hamilton, *loc. cit.*), males tended to wander more than females and to shift their home range more often.

The largest monthly range recorded was 0.28 of an acre used by a female in March, 1951, and calculated on the basis of four captures. The largest monthly range of a male was 0.25 of an acre for a vole caught eight times in November, 1950. The smallest monthly range was 0.02 of an acre; several individuals of both sexes were restricted to areas of this size. Juveniles, not included in the home range study, were usually restricted to 0.01 or, at most, 0.02 of an acre. Seasonal differences in the sizes of home ranges were not significant. However, the voles caught in the winter often enough to be used for home range studies were too few for a thorough study of seasonal variation in the size of home ranges.

One female was captured 22 times in the seven-month period of October, 1950, to April, 1951. She used an area of 0.83 of an acre, but this actually comprised two separate ranges. From October, 1950, through December, 1950, she was taken 17 times within an area of 0.12 of an acre; and from January, 1951, to April, 1951, she was taken five times within an area of 0.15 of an acre. The largest area assumed to represent one range of a female was 0.38 of an acre, recorded on the basis of six captures in three months. The largest area encompassed by the record of an individual male was 0.41 of an acre. He, too, shifted his range, being taken five times on an area of 0.07 of an acre and twice, two months later, on an area of 0.09 of an acre. Presumably, the remainder of his calculated total range was used but little, or not at all. The largest single range of a male was 0.36 of an acre, calculated on the basis of 18 captures in seven months. The smallest total range for both sexes was 0.02 of an acre.

Many voles shifted their home range and a few did so abruptly. The large range of a female vole, described above and plotted in Fig. 6, indicated an abrupt shift from one home range to another. More common is a gradual shift as indicated by the range of the male shown in Fig. 7. Large parts of each monthly range of this vole overlapped the area used in other months but his center of activity shifted from month to month.

That home ranges overlapped was demonstrated by frequent capture of two or more individuals together in the same trap. No territoriality has been reported in any species of *Microtus*, to my knowledge, and my voles showed no objection to sharing their range. Voles taken from the field into the laboratory lived together in pairs or larger groups without much friction.

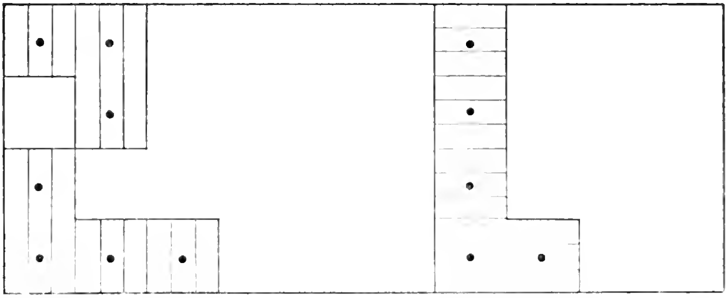


FIG. 6. Map with cross-hatched areas showing the range of vole # 20 (female). Dots show actual points of capture at permanent trap stations 30 feet apart. Vertical lines mark area in which vole was taken 17 times in October and November, 1950. Horizontal lines mark area in which vole was taken five times in March and April, 1951. This vole was not captured in December and January.

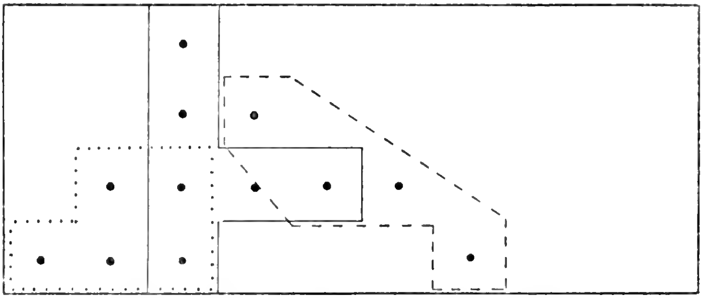


FIG. 7. Map showing range of vole # 52 (male) with seeming shifts in its center of activity. Dots show actual points of capture at permanent trap stations 30 feet apart. Solid line encloses points of six captures in October and November, 1950. Broken line encloses points of five captures in February and March, 1951. Dotted line encloses points of nine captures in April, May and June, 1951.

Definable systems of runways and home ranges were not coextensive. Runway systems tended to merge, as described later in this report, and relationships between them and home range were not apparent. Home ranges had no characteristic shape.

LIFE HISTORY

Reproduction

Reproductive activity might have been measured in a number of ways. Three indicators were tested: the percentage of females gravid or lactating, the percentage of juveniles in the month following the sampling period, and the percentage of females with a vaginal orifice in the sampling period. The condition of vagina proved to be most useful. Whether or not there is a vaginal cycle in *Microtus* is uncertain. Bodenheimer and Sulman (1946:255-256) found no evidence of such a cycle, nor did I in my work with laboratory animals at Lawrence. How much the artificial environment of the laboratory affected these findings is unknown. The presence of an orifice seemed to indicate sexual activity (Hamilton, 1941:9). The percentage of gravid females in the population could not be determined accurately by a live-trapping study and was not useful in this investigation. The percentage of juveniles trapped in the month following the sampling period tended to follow the curve of the percentage of adult females with a vaginal orifice. The ratio of trapped juveniles to adults trapped was a poor indicator of reproductive activity. Juveniles were caught in relatively small numbers because of their restricted movements, and no way to determine prenatal and juvenal mortality was available.

Reproductive activity continues throughout the year. Within the thirty-month period for which data were obtained, December and January showed the lowest percentages of females with vaginal orifices (Fig. 8). The other months all showed higher levels of reproductive activity with a slight peak in the August-September-October period in both 1950 and 1951. In the species of *Microtus* that are found in the United States, such summer peaks of breeding seem to be the rule (Blair, 1940:151; Gunderson, 1950:17; Hamilton, 1937b; 785). Jameson (1947:147) worked in the same county where my field study was made and found that the high point of reproduction was in March, although his samples were too small to be reliable. The peak of reproductive activity slightly preceded the highest level of population density in each year (Fig. 8).

A marked reduction in the percentage of females having vaginal orifices was observed in the unusually dry summer of 1952. The rate of reproduction was found to be positively correlated with rainfall (Fig. 9). Correlation coefficients were higher in each case when the amount of rainfall in the month preceding each sampling period was used instead of that in the month of the sample. This suggested that the rainfall exerted its influence indirectly through its effect on plant growth. Bailey (1924:530) reported that a reduction in either the quantity or quality of food had a depressing effect on reproduction. Drought, such as occurred in 1952, would certainly have a depressing effect on both. The critical factor seems to be the supply of new, actively growing shoots available to the voles for food rather than the total amount of vegetation. As far as could be determined from the small sample of males examined, their fecundity was not affected by rainfall. Some decrease in the percentage of males that were fecund was noted in the winter and was reported also by Jameson (1947:145) but most of the males in any sample were fecund. Thus any depression in the reproductive rate was due to loss of fecundity by females. This was in agreement with reports in the literature on the subject (Baker and Ransom, 1932a: 320; 1932b:43).

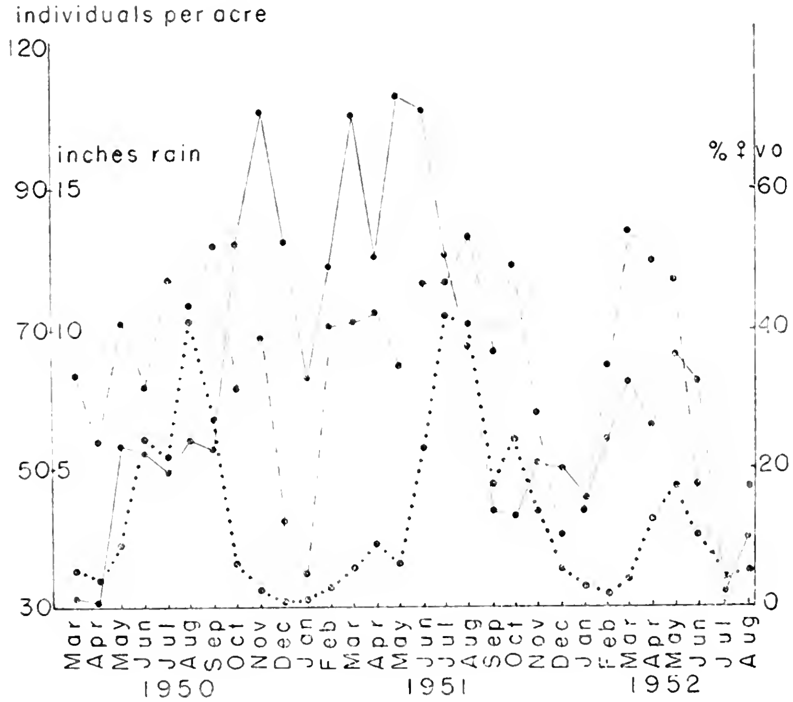


Fig. 8. Variations in density and reproductive rate of voles, with variation in monthly precipitation. Abnormally low rainfall in 1952 caused a decrease in breeding activity and eventually in the numbers of voles. The solid line indicates the number of voles per acre, the broken line the percentage of females with a vaginal orifice and the dotted line the inches of rainfall.

The correlation coefficient between rainfall and the percentage of adult females with a vaginal orifice was 0.53. This was considered to be surprisingly high in view of the expected effects on the breeding rate of temperature, seasonal diet variations and whatever rhythms were inherent in the voles. When only the summer months were considered the correlation coefficient between rainfall and the percentage of adult females with a vaginal orifice was 0.84. This indicated that, during the season when breeding was at its height, rainfall was a factor in determining the rate of reproduction and when rainfall was scarce, as in the summer of 1952, it seemed to be a limiting factor (Fig. 9).

Of the total captures 20.6 per cent involved more than one individual.

When the distribution of these multiple captures was graphed for the period of study, a high correlation between the percentage of captures that were multiple and the percentage of females with a vaginal orifice ($r = 0.70$) was found. An even higher correlation ($r = 0.76$) was observed between the percentage of captures that were multiple and the population density. The higher percentage of multiple captures may have been largely a result of fewer available traps per individual on the area and thus only indirectly related to the rate of reproduction.

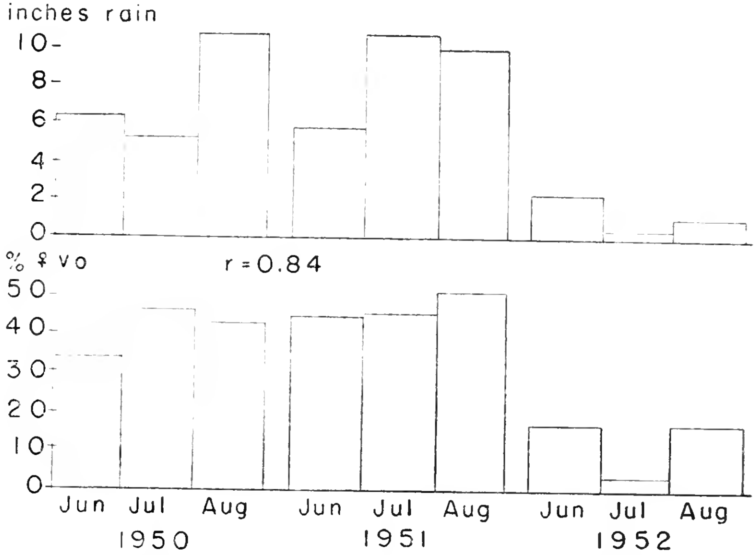


Fig. 9. Comparison between monthly rainfall and reproductive rate of voles in summer. The dry summer of 1952 caused a notable decrease in reproductive activity. The correlation coefficient between rainfall and the percentage of females with a vaginal orifice was 0.84.

Of the multiple captures, 66 per cent involved both sexes. The correlation coefficient between the percentage of captures involving both sexes and the level of reproductive activity was 0.58. Among those pairs of individuals caught together more than once, 61 per cent were composed of both sexes. Among those pairs taken together three or more times 76 per cent were male and female and among those pairs taken together four or more times 80 per cent were male and female. When adult voles stayed together any length of time their relationship usually appeared to be connected with sex. Family groups were also noted, as pairs were often trapped which seemed to be mother and offspring. A lactating female would sometimes enter a trap even after it had been sprung by a juvenile, presumably her offspring, or a juvenal vole would enter a trap after its mother had been captured. Such family groups persisted only until the young voles had been weaned.

The youngest female known to be gravid was 26 days old and weighed 28 grams. During summer most of the females were gravid before they were six weeks old, although females born in October and after were often more than 15 weeks old before they became gravid. The youngest male known to be fecund was approximately six weeks old. Male fecundity was determined as described by Jameson (1950). Difference in the age of attainment of sexual maturity serves to reduce the mating of litter mates (Hamilton, 1941:7) and has been noticed in various species of the genus *Microtus* by several authors (Bailey, 1924:529; Hatfield, 1935:264; Hamilton, *loc. cit.*; Leslie and Ransom, 1940:32).

For 35 females, each of which was caught at least once each month for ten consecutive months or longer, the mean number of litters per year was 4.07. Certain of the more productive members of the group produced 11 litters in 16 months. *M. ochrogaster* seems to be less prolific than *M. pennsylvanicus*. Bailey (1924:528) reported that one female meadow vole delivered 17 litters in 12 months. Hamilton (1941:14) considered 17 litters per year to be the maximum and stated that in years when the vole population was low the females produced an average of five to six litters per year. In "mouse years" the average rose to eight to ten litters per year. During this study several females delivered two or more litters in rapid succession. This was noted more frequently in spring and early summer than in other parts of the year. Those females which produced two or three litters in rapid succession in spring and early summer often did not litter again until fall. Postparous copulation has been observed in *M. pennsylvanicus* by Bailey (1924:528) and Hamilton (1940:429; 1949:259) and probably occurs also in *M. ochrogaster*.

The gestation period was approximately 21 days, the same as reported for *M. pennsylvanicus* (Bailey, *loc. cit.*; Hamilton, 1941:13) and *M. californicus* (Hatfield, 1935:264). A more precise study of the breeding habits of *M. ochrogaster* failed to materialize when the voles refused to breed in captivity. Fisher (1945:437) also reported that *M. ochrogaster* failed to breed in captivity although *M. pennsylvanicus* (Bailey, 1924) and *M. californicus* (Hatfield, 1935) reproduced readily in the laboratory.

Litter Size and Weight

In the course of this study 65 litters were observed. The mean number of young per litter was 3.18 ± 0.24 and the median was three (Fig. 10.) Three litters contained but one individual and the largest litter contained six individuals. Other investigators have reported the number of young per litter in *M. ochrogaster* as three or four (Lantz, 1907:18) and 3.4 (1-7) (Jameson, 1947:146). *M. pennsylvanicus* seems to have larger litters. Although Poiley (1949:317) found the mean size of 416 litters to be only 3.72 ± 0.18, both Bailey (1924:528) and Hamilton (1941:15) found five to be the commonest number of young per litter in that species. Leslie and Ransom (1940:29) reported the average number of live births per litter to be 3.61 in the British vole, *M. agrestis*. Selle (1928:96) reported the average size of five litters of *M. californicus* to be 4.8. Hatfield (1935:265), working with the same species, found that litter size varied directly with the age of the female producing the litter. He reported litters of young females as two to four young per litter and of older females as five to seven young per litter. In the litters of *M. ochrogaster* that I examined, young females did not have more than three young and usually had but two. However, older females had litters of one, two and three often enough so that no relationship, as described above, was indicated clearly.

No seasonal variation in litter size was noted. The mean size of the litters in 1950, 2.68 ± 0.30, was significantly lower than that found in 1951 (3.76 ± 0.20) but neither differed significantly from the mean size of litters in 1952 (3.35 ± 0.66). The lower mean size of litters was in part coincidental with a high population level and the higher mean of the two later years was in part coincidental with a low population level. Since a sharp break in the curve for population density occurred after the flood in July, 1951, the litters were arranged in pre-flood and post-flood categories for study. Pre-flood litters averaged 3.07 ± 0.28 young per litter whereas post-flood litters averaged 3.34 ± 0.48. This difference was not significant. Increase in litter size, if it had actually occurred, might have been a response to the increasing food supply and lower population density after the flood.

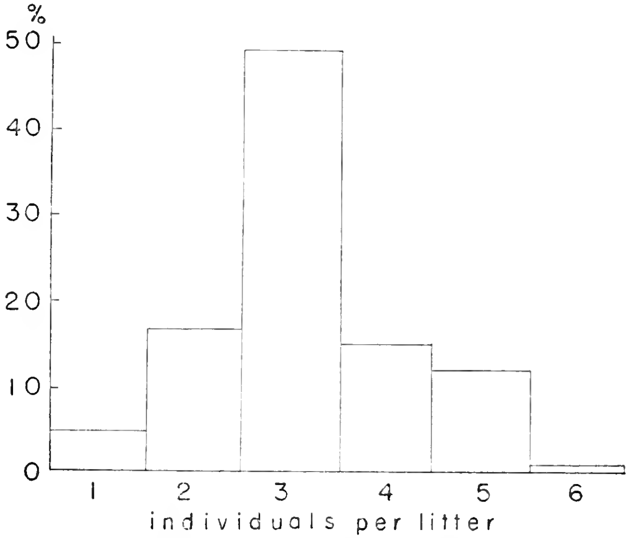


FIG. 10. Distribution of litter size among 65 litters of voles.

A difference in the mean number of young per litter was noted for those litters delivered in traps as compared with those delivered in captivity and the numbers of embryos examined in the uterus. The mean number of embryos per female was higher than the mean number of young per litter delivered in captivity and the mean number of young per litter delivered in traps was lower than in those delivered in captivity. The differences were not statistically significant. In some instances females that delivered young voles in traps may have delivered others prior to entering the trap or the mother or her trapmates may have eaten some of the newborn voles before they were discovered.

The mean weight of 16 newborn (less than one day old) individuals was 2.8 ± 0.36 grams. No other data on the weight of newborn *M. ochrogaster* were found in the literature but this mean was close to the 3.0 grams (Bailey, 1924:530) and 2.07 grams (Hamilton, 1937a:504; 1941:10) reported for *M. pennsylvanicus* and to the 2.7 grams (Selle, 1928:97) and 2.8 grams (Hatfield, 1935:268) reported for *M. californicus*. No correlation between the weight of the individual newborn vole and the number of voles per litter was observed.

Although the ratio of the average weight of newborn voles to the average weight of an adult female was approximately equal for *M. pennsylvanicus* and *M. ochrogaster*, the ratio of the weight of a litter to the average weight of an adult female was larger in the eastern meadow vole because the mean litter size was larger. Perhaps this is related to the more productive habitat in which the eastern meadow vole is ordinarily found.

Size, Growth Rates and Life Spans

The mean weight of adult voles during the period of study was 43.78 grams. The females averaged slightly heavier than the males but the overlapping of weights was so extensive that sexual difference in weight could not be affirmed. The difference observed was less in December and January when gravid females were rare, suggesting that the difference was due, at least in part, to pregnancy. Jameson (1947:128) found, for a sample of 50 voles, a mean weight of 44 grams and a range of 38 to 58 grams. The range in the adult voles I studied was much greater, from 25 to 73 grams. In part, this increase in the range of adult weights was due to a much larger sample.

During the unusually dry summer of 1952, a notable reduction in the mean weight of adults was recorded (Fig. 11). The correlation coefficient between the mean weight of adults and the amount of rainfall for the summer months was 0.68. It seems reasonable to attribute the drop in mean weight to an

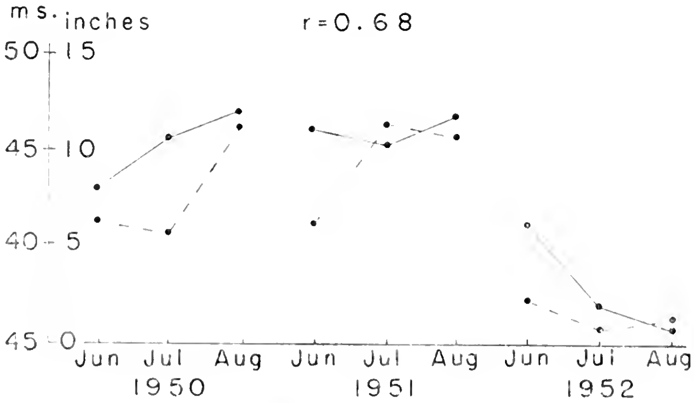


FIG. 11. Relationship between rainfall and the mean weight of adult males in summer. The abnormally low rainfall in the summer of 1952 was accompanied by a decrease in mean weight. The solid line represents mean weight and the broken line rainfall. The correlation coefficient between the two was 0.68.

alteration of plant growth due to decreased rainfall. Some of the reduction in mean weight was due to the loss of weight in older individuals but most of it was due to the failure of voles born in the spring to continue growing.

No data on the growth rate of *M. ochrogaster* were found in the literature. According to the somewhat scanty data from my study, secured from observations of individuals born in the laboratory, young voles gained approximately 0.6 of a gram per day for the first ten days, approximately one gram per day up to an age of one month, and approximately 0.5 of a gram per day from an age of one month until growth ceases. This growth rate was especially variable after the voles reached an age of thirty days. The growth rate approximates those described for *M. pennsylvanicus* (Hamilton, 1941:12) and for *M. californicus* (Hatfield, 1935:269; Selle, 1928:97). Although the data were inadequate for a definite statement, I gained the impression that there was no difference between the sexes in growth rate. In general, young voles grow most rapidly in the April-May-June period and least rapidly in mid-winter. Several voles, born in late autumn, stopped growing while still far short of adult size and lived through the winter without gaining weight, then gained as much as 30 per cent after spring arrived (Fig. 12).

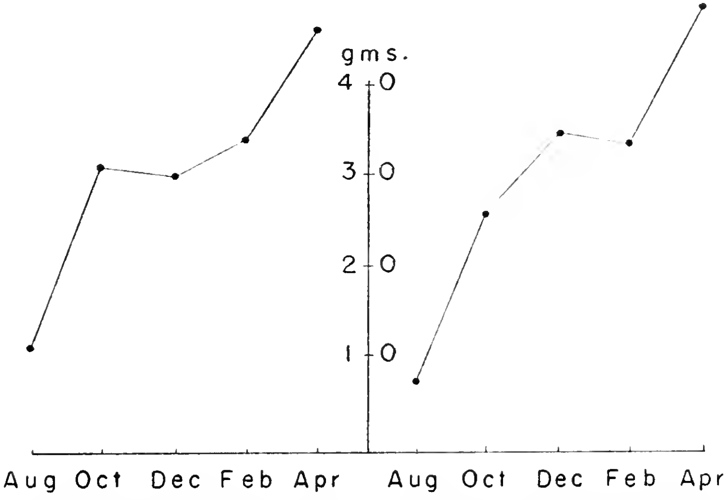


FIG. 12. Growth rates of two voles selected to show typical growth pattern of voles born late in the year. Growth nearly stops in winter and is resumed in spring.

The recorded life spans of most voles studied were less than one year. No accurate mean life span could be determined. Leslie and Ransom (1940:46), Hamilton (1937a:506) and Fisher (1945:436) also found that most voles lived less than one year. Leslie and Ransom (*op. cit.*: 47) reported a mean life span of 237.59 ± 10.884 days in voles of a laboratory population. In the present study one female was trapped 624 days after first being captured; another female was trapped 617 days after first being captured; and a male was trapped 611 days after first being captured. The two females were subadults when first captured. The male was already an adult when first captured; consequently its life span must have exceeded 650 days. No evidence of any decrease in vigor or fertility was observed to accompany old age.

Of the 45 marked voles snap-trapped in August of 1952, 21 had been captured first as juveniles. The ages of these voles could be estimated within a few days, and the series presented a unique opportunity for studying individual and age variation. Only individuals weighing less than 18 grams when first captured were used, and their ages were estimated according to the growth rate described above. Howell (1924) reported an analysis of individual and age variation in a series of specimens of *Microtus montanus*, and Hall (1926) studied the changes due to growth in skulls of *Otospermophilus grammarus beecheyi*. The series of specimens described here differs from those of Hall and Howell, and from any other collection known to me, in the fact that the specimens are of approximately known age and drawn from a wild population.

Unfortunately, this sample was small, and the distribution of the specimens among age groups left much to be desired. No specimens less than one and one-half months old were taken and only a few individuals older than four and one-half months. Table 3 shows the age distribution. The small size of the sample and the absence of juveniles were due, partly, to the unusually dry weather in the summer of 1952. The reduction in the rate of reproduction, caused by drought (as described elsewhere in this paper), reduced the populations and the percentage of juveniles to low levels.

TABLE 3. DISTRIBUTION AMONG AGE GROUPS OF 21 VOLES USED IN THE STUDY OF VARIATION DUE TO AGE

Age in months	1½	2	2½	3	3½	4	4½	6	12
No. of individuals	1	4	5	1	3	2	3	1	1

In the series of voles studied, ten individuals were in the process of molting from subadult to adult pelage. Jameson (1947:131) reported the molt to occur between eight and 12 weeks of age and selected 38 grams as the lower limit of weight of adults. I also found all voles molting to be between eight and 12 weeks old but found none so large as 38 grams without full adult pelage. This may have been, in part, due to the dry weather delaying or inhibiting growth. Because of the small size of the sample and the influence of the unusual weather conditions, no conclusions concerning normal molting were drawn from the data described below. They are presented only as a description of a small sample drawn from a single population at one time. Table 4 summarizes these data.

TABLE 4. MEAN SIZES AND AGES OF VOLES MOLTING FROM SUBADULT TO ADULT PELAGE

	Weight	Body length minus tail	Condylo-basilar length	Age
Six males	32.67 gms. (30-36)	106.16 mm. (96-116)	23.78 mm. (23.2-24.4)	9.67 wks. (8-12)
Four females	29.0 gms. (28-30)	100.25 mm. (98-102)	23.45 mm. (23.5-23.8)	10.5 wks. (8-12)
Ten voles	31.2 gms. (28-36)	103.8 mm. (96-116)	23.73 mm. (23.2-24.4)	10.0 wks. (8-12)

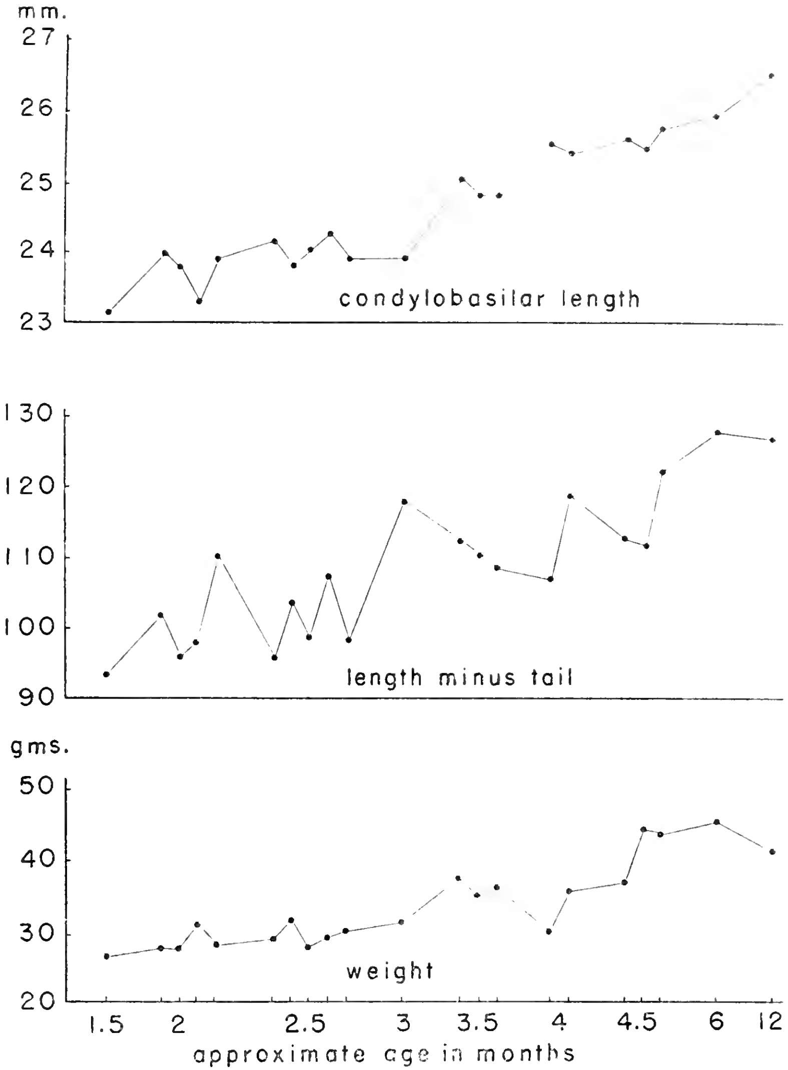
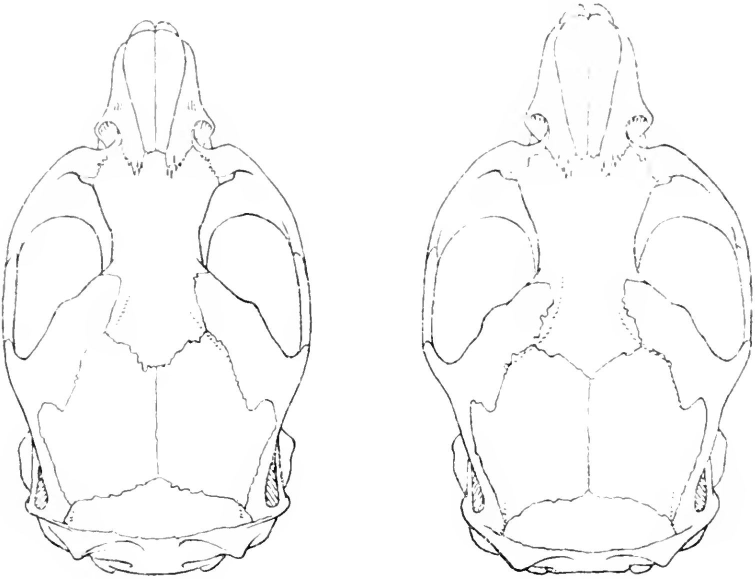
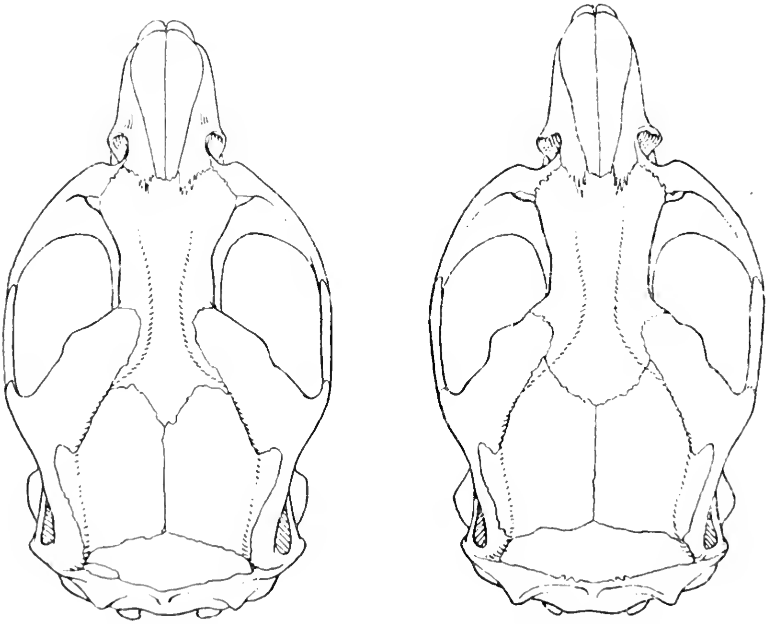


Fig. 13. Graphs of the condylobasilar lengths, body lengths and weights of a series of voles of known age. Within each age group, the youngest vole is on the left in the graphs.



1½ months

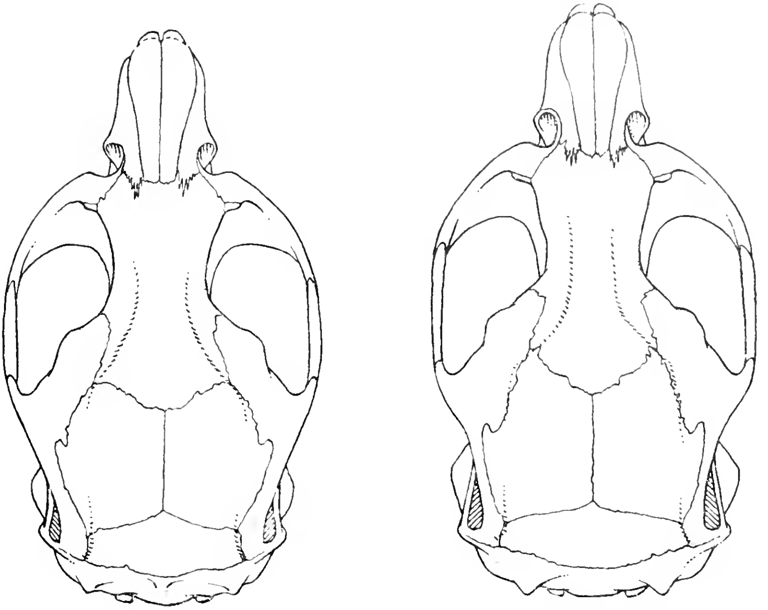
2½ months



4 months

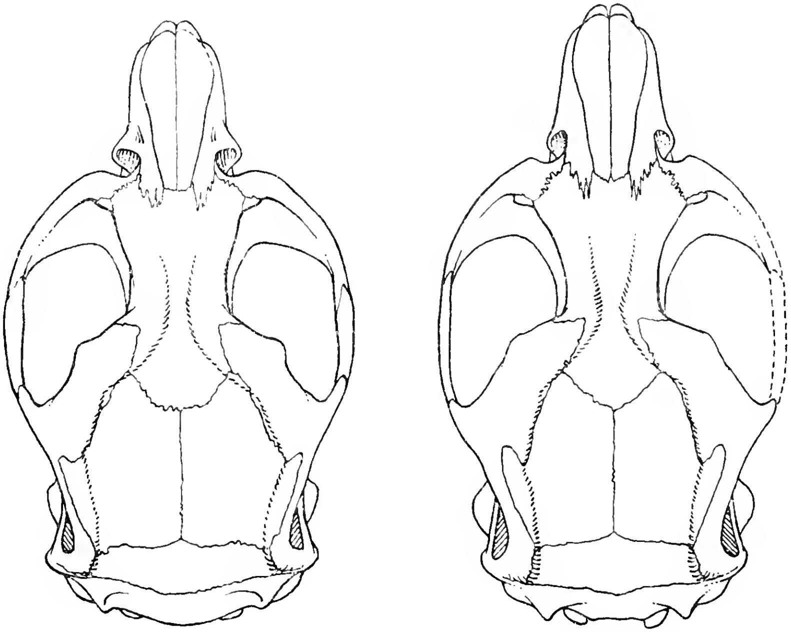
4½ months

FIG. 14. Dorsal views of



3 months

3½ months

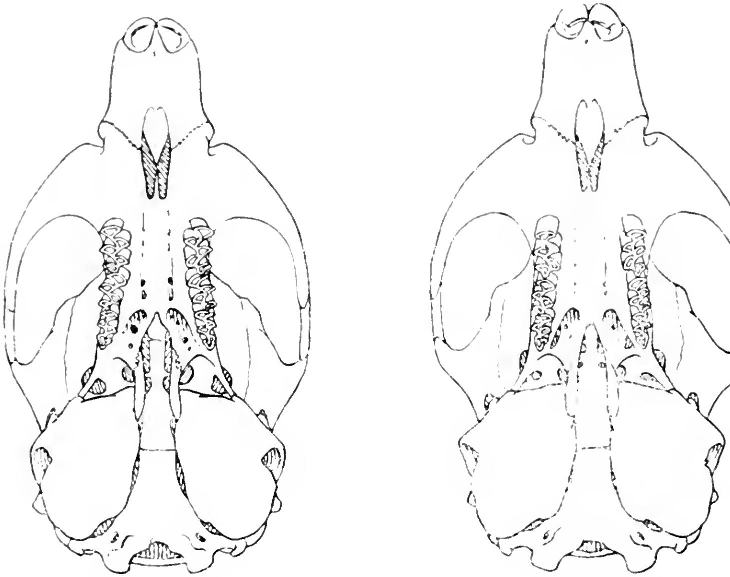


6 months

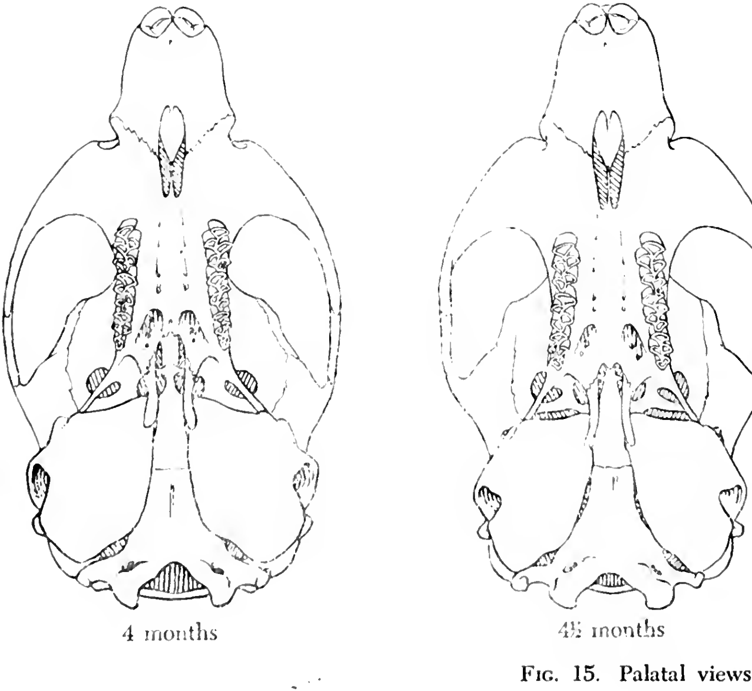
12 months

skulls of voles of known age. All × 8.

3—9225

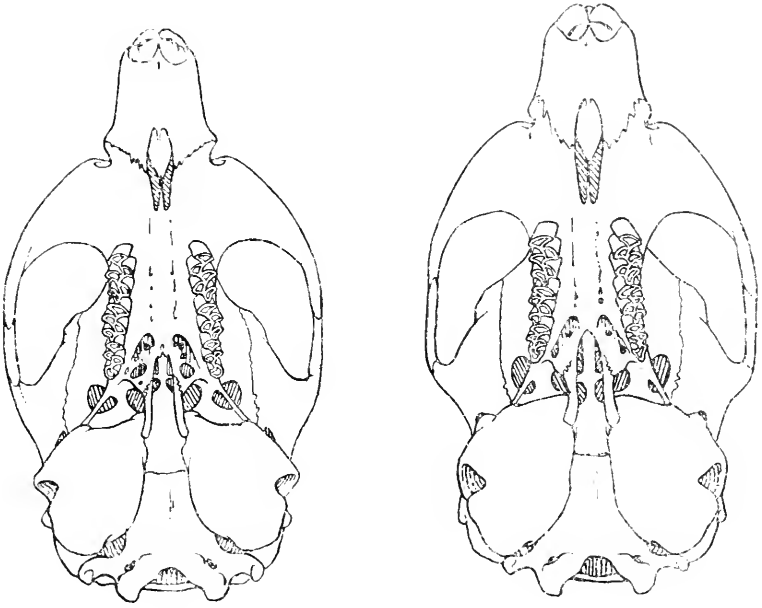


1½ months 2½ months



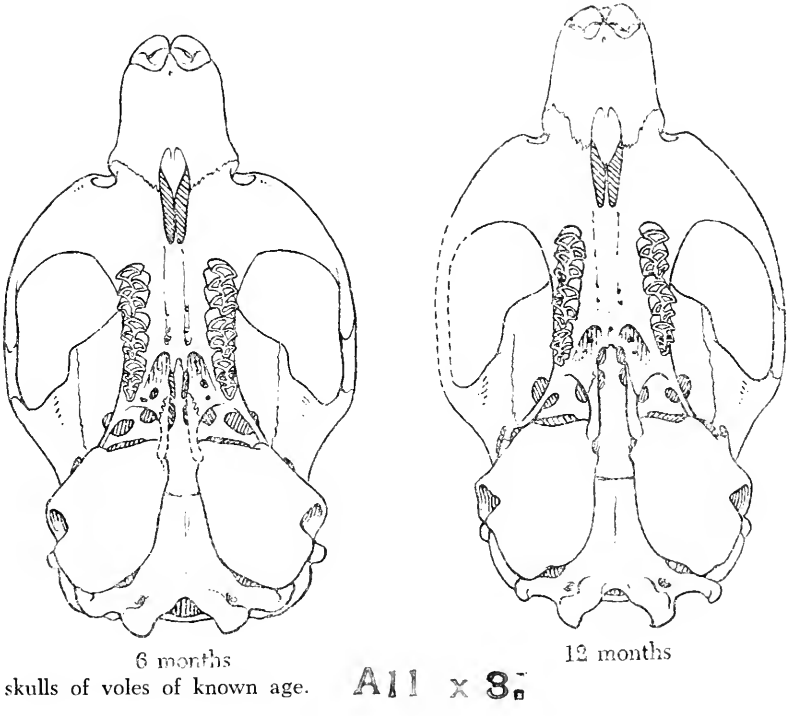
4 months 4½ months

FIG. 15. Palatal views of



3 months

3½ months



6 months

12 months

skulls of voles of known age.

All x 3.

The mean age of the ten voles molting was ten weeks (8-12). Six males averaged 9.67 weeks, almost a week younger than four females, who averaged 10.5 weeks. The difference in age at time of molting between the sexes was not significant. Differences between the sexes in other characteristics to be described also lacked significance. Mean weights at the time of molting were: males, 32.67 gms. (30-36); females, 29.0 gms. (28-30); and all individuals, 31.2 gms. (28-36). Because a piece of the tail of each vole had been removed in marking, the total length of the voles could not be determined. Body length, excluding tail, was used. Howell (1924:986) found this measurement subject to less individual variation than total length and thought body length was probably a better indicator of age. Mean body length at the time of molting was 103.8 mm. (96-116). Males averaged longer than females and were also more variable. The mean body length of males was 106.16 mm. (96-116) and that of females was 100.25 mm. (98-102).

Of the subadults showing no signs of molting, none was above the mean age of molting. Twenty-five per cent of them were longer and heavier than the mean length and weight of those that were molting. Of the 20 adults in the series, one was below the mean weight of molting and one was shorter than the mean length of molting.

When Howell (*op. cit.*:1014) studied skulls of *Microtus montanus* he found that the condylobasilar length was the most satisfactory means for arranging his series of specimens according to their age. When the skulls of my series were arranged according to their age (as determined from trapping records) the graph of the condylobasilar lengths showed a clear, though not perfect, relationship to age (Fig. 13). No separation of sexes was made because the sample did not permit it. In Fig. 13 graphs of weight, as determined in the field, and of length (excluding tail) also were included because they are the most easily measured characters of live voles. The graphs indicate individual variation in these characters which limits their usefulness in determining age.

When other cranial measurements, and ratios of pairs of measurements, were plotted in the same order, individual variation obscured some of the variation due to age and the curves resembled those of weight and length of body rather than that of condylobasilar length. When the cranial measurements were averaged for the age groups the curves showed a relationship to age but the relationship of mean measurements is of little use in determining the age of individual specimens. The data described above indicated that a study of the relationship of the condylobasilar length and age in a large sample might provide useful information.

Anyone who has examined mammalian skulls knows of many other characters which vary with age but which are difficult to measure and describe with precision. Figs 14 and 15 are drawings of skulls of voles of known age. The most obvious change, related to aging, evident in the dorsal view of the skulls (Fig. 14) is the increasing prominence and closer approximation of the temporal ridges in older specimens. The lambdoidal ridge is also more prominent in older voles, and their skulls have a generally rougher and more angular appearance. The individual variation evident in these ridges is probably due to variations in the development of the muscles operating the jaws (Howell, 1924:1003). There is an increased flattening of the roof of the skull of older voles.

From a palatal view (Fig. 15) the skulls of voles also showed age variation which was apparent but not easily correlated with precise age. The median ridge on the basioccipital bone increases in prominence in older voles. The shape of the posterior margin of the palatine bones changes from a V-shape to a U-shape. On the skull of the oldest (12 months) vole the pterygoid processes are firmly fused to the bullae, a condition not found in any of the other specimens. The anterior spine of the palatine approaches the posterior projection of the premaxillae more closely as age increases and, in the oldest vole is firmly attached and forms a complete partition separating the incisive foramina.

Tooth wear during the life of a vole causes a considerable variation in the enamel patterns, especially of the third upper molar. Howell (1924:1012) considered such variation to be independent of age, but Hinton (1926:103) related the changes to age and interpreted them as a recapitulation of the evolution of microtine molars. In my series, an indentation on the medial margin of the posterior loop of the third upper molar seemed to be related to age. This indentation was absent in the youngest vole (one and one-half months), absent or indefinite in those voles less than 3½ months of age, and progressively more marked in the older voles.

Food Habits

The prairie vole, like other members of the genus *Microtus,* feeds mostly on growing grass in spring and summer. Piles of cuttings in the runways are characteristic sign of the presence of voles. The voles cut successive sections from the bases of grasses until the young and tender growing tips are within reach. The quantity of grass destroyed is greater than that actually eaten, a fact which will have to be considered in any attempt to evaluate the effects of voles upon a range.

In all piles of cut plants that were examined, *Bromus inermis* was the most common grass, and *Poa pratensis* was the grass second in abundance. These were, by far, the most common grasses present on the areas studied; in most places, *B. inermis* was dominant. Other grasses present on the areas were occasionally found in the piles of cuttings. Jameson (1947:133-136) found no utilization of *B. inermis* by voles but that grass was present in a relative abundance of only one per cent in the areas studied by him. The voles that he studied ate alfalfa in large amounts and alfalfa was, perhaps, the most common plant on the particular areas where his voles were caught. Seemingly, the diet of voles is determined mostly by the species composition of the habitat.

Other summer foods included pokeberries, blackberries and a few forbs and insects. Forbs most commonly found in the piles of cuttings were the leaves of the giant ragweed (younger plants only) and dandelion. Insect remains were found in the stomachs of voles killed in summer and occurred most frequently in those killed in August and September. At no time did insects seem to be a major part of the diet but they were present in most vole stomachs examined in late summer. Laboratory experiments with summer foods gave inconclusive results but suggested that the voles chose grasses on the basis of their growth stage rather than according to their species. Young and tender grasses were chosen, regardless of species, when various combinations of *Triodia flava, Bromus inermis* and *Poa pratensis* were offered to the voles. At times the voles showed a marked preference for dandelion greens, perhaps because of their high moisture content; the voles' water needs were satisfied mostly by eating such succulent vegetation.

Winter foods consisted of stored hay and fruits and of underground plant parts. *Bromus inermis* made up nearly all of the hay and was stored in lengths of up to ten inches in underground chambers specially constructed for storage. Underground parts of plants were reached by tunnelling and were an especially important part of the voles' diet in January and February. The fruit of *Solanum carolinense* was eaten throughout the winter and one underground chamber, opened in February, 1952, was packed full of these seemingly unsavory fruits. Fisher (1945:436), in Missouri, found this fruit to be an important part of the winter diet of voles. An occasional pod of the honey locust tree was found partly eaten in a runway. Fitch (1953, *in litt.*) often observed girdling of honey locust and crab apple (*Pyrus ioensis*) root crowns on the Reservation but I saw no evidence of bark eating, perhaps because my study plots were mostly grassland. On two occasions when two voles were in the same trap one of them was eaten. In both traps, all of the bait had been eaten and the captured voles probably were approaching starvation. Because the trapping procedure offered abundant opportunity for cannibalism, the low frequency of its occurrence suggested that it was not an important factor in satisfying food requirements under normal conditions.

Runways and Nests

Perhaps the most characteristic sign of the presence of *Microtus ochrogaster* were their surface runways and underground tunnels. Only rarely was a vole observed to expose itself to full view. When a trapped vole was released it immediately dove out of sight into a runway. Once in a runway, the vole showed no further evidence of alarm and was usually in no hurry to get away. The runways seemed to provide a sense of security and the voles were familiar with their range only through runway travel. The urge to seek a runway immediately when exposed has obvious survival value.

Surface runways were usually under a mat of debris. In areas where debris was scanty or lacking, runways were usually absent. Jameson (1947: 136) reported that in alfalfa and clover fields the voles did not make runways as they did in grassland, even in fields where trapping records showed voles to be abundant. Typical surface runways are approximately 50 mm. wide, only slightly cut into the ground and bare of vegetation while in use. Usually they could be distinguished from the runways of the pine vole, which were cut more deeply into the ground, and those of the cotton rat which were wider and not so well cleared of vegetation. Some runways ended in surface chambers and some of these were lined with grass. Their size varied from a diameter of 90 mm. to 250 mm. and they seemed to be used primarily for resting places.

A runway system usually consisted of a long, crooked runway and several branches. Two typical systems are illustrated in Fig. 16. The runway systems often were not clearly limited; they merged with other systems more or less completely. One map showed a runway system extending across 140 square meters and including 12 underground burrows. All of these runways seemed to be part of a single runway system but the system probably was used by more than one vole or family group of voles. Sixteen of the 22 maps that were made extended across areas between 50 and 90 square meters. One map, mentioned above, was larger and the remaining five smaller. The smallest extended across only 20 square meters. Of course, the area encompassed by a set of runways changed almost daily, as the voles extended some runways, added some and abandoned others in the course of their daily travels.

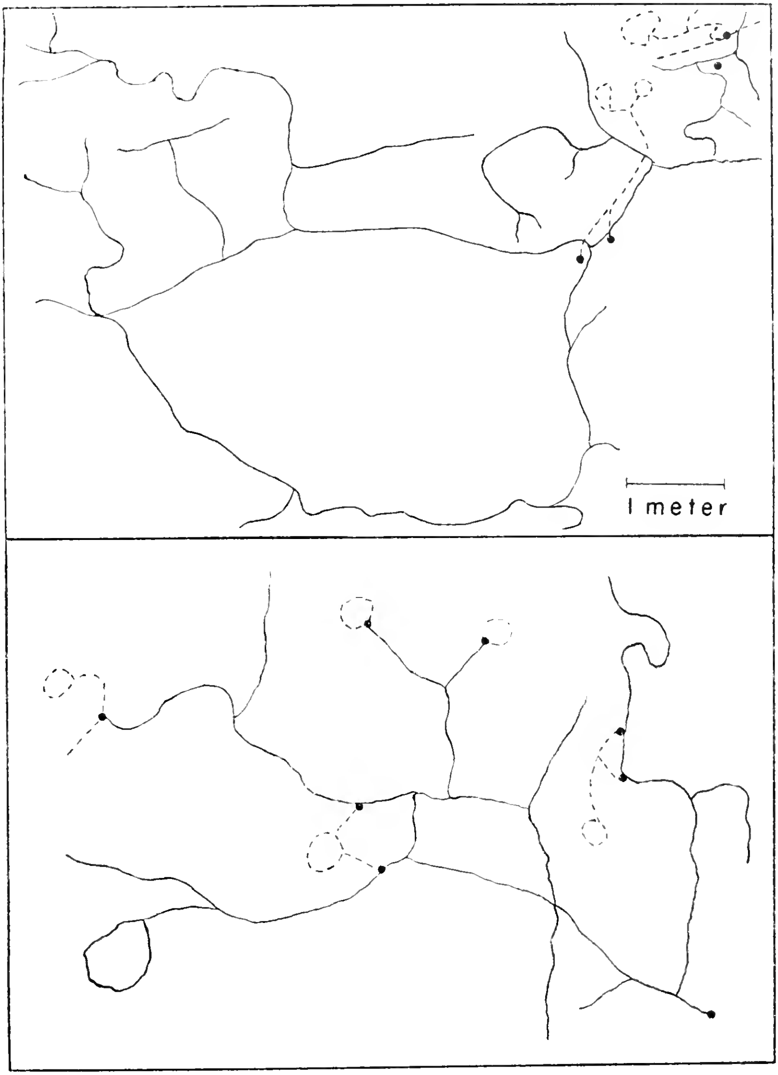


Fig. 16. Maps of runway systems of the prairie vole. The runways follow an irregular course and are frequently changed. The solid lines represent surface runways and the dotted lines underground passages.

Each runway system contained underground nests. These were in chambers from 70 mm. to 200 mm. below the surface and were up to 200 mm. in diameter. Most systems that were mapped had from two to six of these burrows. Most of these were lined with dried grass and seemed to be used for delivering and nursing litters. Each burrow was connected to a surface runway by a tunnel. Often the tunnel was short and the hole opened almost directly into the burrow from the surface runway. Others had tunnels several meters long. Jameson (1947:137) reported every burrow to have two connections with the surface. In the present study, however, I found three arrangements in approximately equal frequency of occurrence: (1) one hole to one tunnel leading to a burrow; (2) two holes to two short tunnels which joined a long tunnel leading to a burrow; and (3) two separate tunnels from the surface to a burrow. The size, depth and number of underground burrows in the systems that I studied varied and so did those reported in the literature. Jameson (*loc. cit.*) found burrows in eastern Kansas as deep as 18 inches, far deeper than any found in my study. Fisher (1945:435) reported none deeper than five inches in central Missouri. The soil data in my study, as well as in the two reports cited immediately above, were not adequate to permit conclusions, but the type and condition of the soil probably determine the extent of burrowing by the voles of any given locality.

The number of voles using a runway system at one time was difficult to ascertain. In one system, however, four adult individuals were trapped in a ten day period. In August, 1952, at the conclusion of the live-trapping program, a runway system was mapped which had included two trapping stations. In the preceding ten days, four adult voles (three males and one female) had been taken in both traps. During that time, therefore, the runway system was shared by at least four voles. The voles used an area that was considerably larger than that encompassed by any one runway system, a fact obvious when the sizes of home ranges as computed from trapping data were compared with the sizes of the runway systems mapped. A runway system seemed not to be a complete unit, but was only a part of the network of runways used by a single individual.

Activity

Although no special investigation of activity was made, some conclusions concerning it were apparent in the data gathered. There have been a few laboratory studies of the activity pattern of *Microtus* by various methods. Calhoun (1945:256) reported *M. ochrogaster* to be mainly nocturnal with activity reaching a peak between dark and midnight and again just before dawn. Davis (1933:235), working with *M. agrestis*, and Hatfield (1935:263), working with *M. californicus*, both found voles to be more nocturnal than diurnal. In a field study of *M. pennsylvanicus*, Hatt (1930:534) found the species to be chiefly nocturnal, although some activity was reported throughout the day. Hamilton (1937c:256-259, however, reported the same species to be more active in the daytime. Agreement on the activity patterns of these species of *Microtus* has not yet been attained.

From occasional changes in the time of tending a trap line, and from running lines of traps at night a few times in the summer of 1951, I gained the impression that these voles were primarily diurnal. Relatively few of them were caught in the hours of darkness. In summer, however, their activity was mostly limited to the periods between dawn and approximately eight o'clock and between sunset and dark. In colder weather, there was increased activity on sunny days.

PREDATION

Although voles were a common item of prey for many species of predators on the Reservation, no marked effect on the density of the population of this vole could be attributed to predation pressure. Only when densities reached a point that caused many voles to expose themselves abnormally could they be heavily preyed upon. Their normally secretive habits, keeping them more or less out of sight, suggest that they are an especially obvious illustration of the concept that predation is an expression of population vulnerability, rising to high levels only when a population is ecologically insecure, rather than a major factor regulating population levels (Errington, 1935; 1936; 1943; Errington *et al,* 1940).

Scats from predatory mammals and reptiles and pellets from raptorial birds were examined. Most of these materials were collected by Dr. Henry S. Fitch, who kindly granted permission to use them. The results of the study of the scats and pellets are summarized in Table 5. Remains of voles were identified in 28 per cent of the scats of the copperhead snake (*Ancistrodon contortix*) examined. Copperheads were moderately common on the Reservation (Fitch, 1952:24) and were probably important as predators on voles in some habitats. Uhler *et al* (1939:611), in Virginia, reported voles to be the most important prey item for copperheads. A vole was taken from the stomach of a rattlesnake (*Crotalus horridus*) found dead on a county road adjoining the Reservation. Rattlesnakes were present in small numbers on the Reservation but were usually found along rocky ledges rather than in areas where voles were common (Fitch, *loc. cit.*). The rattlesnakes probably were less important as predators on voles than on other small mammals more common in the usual habitat of these snakes. The blue racer (*Coluber constrictor*) was common in grassland situations on the Reservation (Fitch, 1952:24) and twice was observed in the role of a predator on voles; one small blue racer entered a live-trap in pursuit of a vole and another blue racer was observed holding a captured vole in its mouth. The blue racer seems well adapted to hunt voles and probably preys on them extensively. The pilot black snake (*Elaphe obsoleta*) has been reported as a predator on *M. ochrogaster* in the neighboring state of Missouri (Korschgen, 1952:60) and was moderately common on the Reservation (Fitch, *loc. cit.*). *M. pennsylvanicus,* with habits similar to those of *M. ochrogaster,* has been reported as a prey for all of the above snakes (Uhler, *et al,* 1939).

TABLE 5. FREQUENCY OF REMAINS OF VOLES IN SCATS AND PELLETS

Predator	No. of scats or pellets examined	No. containing remains of voles	Percentage
Copperhead	25	7	28
Red-tailed hawk	25	3	12
Long-eared owl	25	18	72
Great horned owl	32	6	19
Crow	25	4	16
Coyote	25	3	12

The red-tailed hawk (*Buteo jamaicensis*), the long-eared owl (*Asio otus*), the great horned owl (*Bubo virginianus*) and the crow (*Corvus brachyrhynchos*) fed on *Microtus*. All four birds were fairly common permanent residents on the Reservation (Fitch, 1952:25). The low density and the strict territoriality of the red-tailed hawk (Fitch, *et al*, 1946:207) prevented it from exerting any important influence on the population of voles, even though individual red-tailed hawks ate many voles. Predation by the long-eared owl was especially heavy; remains of voles were identified in 72 per cent of its pellets examined. Korschgen (1952:39) found remains of voles in 70 per cent of 704 pellets of the long-eared owl. The reason for the heavy diet of *Microtus* seems to be that both the owl and the vole are especially active at dusk. A group of long-eared owls, living near the edge of Quarry Field, probably exerted an influence on the density of the local population of voles because of the high ratio of predator to prey animals. The crows ate some, and perhaps most, of their voles after the animals had died from other causes. Other birds, mostly raptors, occurring in northeastern Kansas and reported to prey on voles include the sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*A. cooperi*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*B. platypterus*), American rough-legged hawk (*B. lagopus*), ferruginous rough-legged hawk (*B. regalis*), marsh hawk (*Circus cyaneus*), barn owl (*Tyto alba*), screech owl (*Otus asio*), barred owl (*Strix varia*) and shrike (*Lanius excubitor*) (Korschgen, 1952:26; 28; 34; 35; 37; McAtee, 1935:9-27; Wooster, 1936:396).

Coyotes, house cats and raccoons were identified as predators on voles in the study areas. Remains of voles were present in 12 per cent of the scats of the coyote (*Canis latrans*) examined. In Missouri, Korschgen (1952:40-43) reported remains of voles in slightly more than 20 per cent of the coyote stomachs that he examined. Fitch (1948:74), Hatt (1930:559) and others have reported other species of *Microtus* as eaten by the coyote. Although coyotes were rarely seen on the Reservation, coyote sign was abundant (Fitch, 1952:29) and coyotes probably ate large numbers of voles. House cats (*Felis domesticus*), seemingly feral, were observed to tour the trap lines on several occasions and were noted by Fitch (*loc. cit.*) as important predators on small vertebrates. Four cats were killed in the course of the study and remains of voles were found in the stomachs of all of them. On several occasions, raccoon tracks were noted following the trap line when the traps had been overturned and broken open, suggesting that raccoons are not averse to eating voles although no further evidence of predation on voles by raccoons was obtained. Fitch (*loc. cit.*) reported raccoons (*Procyon lotor*) to be moderately common on the Reservation. Reports of predation by raccoons on voles are numerous (Hatt, 1930:554; Lantz, 1907:41). The opossum (*Didelphis marsupialis*), common on the Reservation, occasionally eats voles (Sandidge, 1953:99-101). Other mammals which are probably important predators on voles on the Reservation, though no specific information is available, are the striped skunk (*Mephitis mephitis*), spotted skunk (*Spilogale putorius*), weasel (*Mustela frenata*) and the red fox (*Vulpes fulva*). Eadie (1944; 1948; 1952), Shapiro (1950:360) and others have reported that the short-tailed shrew (*Blarina brevicauda*) was an important predator on *Microtus*. Shrews were present on the Reservation but were not trapped often enough to permit study.

The variety of vertebrates preying on voles suggests that they occupy a position of importance in many food chains. Errington (1935:199) and McAtee (1935:4) refer to voles as staple items of prey for all classes of predatory vertebrates. An attempt to evaluate prey species was made by Wooster (1939). He proposed a formula which involved multiplying the density of a species, its mean individual weight, the fraction of the day it was active and the fraction of the year it was active to give a numerical index of prey value. Although his methods of determining population densities would now be considered questionable, the purpose of his investigation merits further consideration. He reported *M. ochrogaster* to be second only to the jack-rabbit (*Lepus californicus*) as a prey species in west-central Kansas.

MAMMALIAN ASSOCIATES

In the course of live-trapping operations several species of small mammals other than *Microtus ochrogaster* were taken in the traps. Also, from time to time, direct observations of certain mammals were made and various types of sign of larger mammals were noted. These records gave a picture of the mammalian community of which the voles were a part. The three associated species which were most commonly trapped were *Sigmodon hispidus, Reithrodontomys megalotis* and *Peromyscus leucopus.* These three species have been commonly found associated with *Microtus* in this part of the country (Fisher, 1945:435; Jameson, 1947:137).

The Texas cotton rat, *Sigmodon hispidus,* was the most commonly trapped associate of the voles between November, 1950, and February, 1952. Although a greater number of individuals of the harvest mouse were taken in a few months, the cotton rat had a greater ecological importance because of its larger size (Figs. 17, 18, 19). The cotton rat was an especially noteworthy member of the community for two reasons. It has arrived in northern Kansas only recently and its progressive range extension northward and westward has attracted the attention of many mammalogists (Bailey, 1902:107; Cockrum, 1948; 1952:183-187; Rinker, 1942b). Secondly, *Sigmodon* has long been considered to be almost the ecological equivalent of *Microtus* and to replace the vole in the southern United States (Calhoun, 1945:251; Svihla, 1929:353). Since the two species are now found together over large parts of Kansas their relationships in the state need careful study.

Both this study and the literature (Black, 1937:197; Calhoun, *loc. cit.;* Meyer and Meyer, 1944:108; Phillips, 1936:678; Rinker, 1942a:377; Strecker, 1929:216-218; Svihla, 1929:352-353) showed that, in general, the habitat needs of *Microtus* and *Sigmodon* were similar. Studies on the Natural History Reservation, both in connection with my problem and otherwise, suggested, however, that *Sigmodon* occurred in only the more productive habitat types used by voles, where the vegetation was relatively high and rank. On the Reservation the cotton rat was found mostly in the lower meadows; they were more moist and had a more luxuriant vegetation than the higher fields. Although a few cotton rats were taken in Quarry Field and still fewer in Reithro Field, the population of those hilltop areas did not approach, at any time, the levels reached on House Field, which produced a more luxuriant cover. Only when the levels of population were exceptionally high did the cotton rats spread into less productive habitats. At all times, there were areas on the Reservation used by *Microtus* which could not support a population of *Sigmodon.*

The cotton rats reacted differently to the floods of July, 1951, than did the voles. Although the population of the cotton rat decreased slightly immediately after the wet period, this decrease was insignificant when compared with the drop in population level of other species of small mammals on the same area. During the autumn of 1951 and until March, 1952, the cotton rat became the most important mammal on the House Field study area in terms of grams per acre (Fig. 17), although the number of cotton rats per acre never matched the density of the voles. A similar, though less pronounced, trend was observed on the Quarry Field study area (Fig. 18). One factor in the success of the cotton rat at this time seemed to be the greater resistance to wetting shown by very young individuals. Few adults (of any species) marked before the heavy rains of July, 1951, were trapped in September, 1951, when trapping was resumed after a lapse of one month. Several subadults and some juvenal

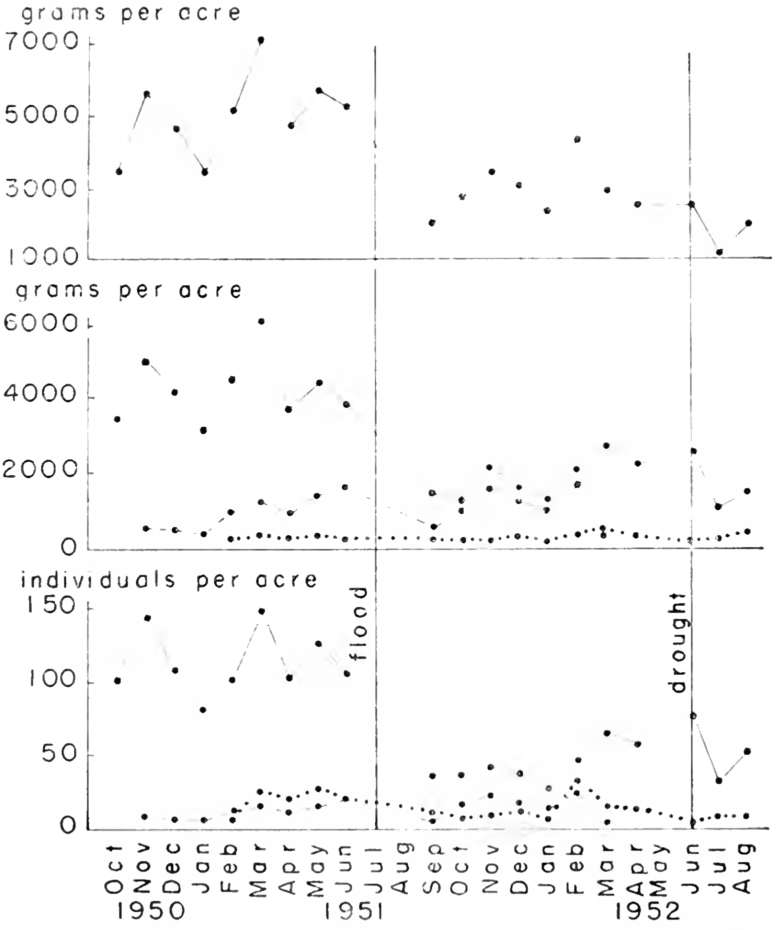


FIG. 17. Variations in density and mass of three common rodents on House Field. The upper graph shows the sum of the biomass of the three rodents. In the two lower graphs the solid line represents *Microtus*, the broken line *Sigmodon*, and the dotted line *Reithrodontomys*.

cotton rats did survive, however, and provided a breeding population from which the area was repopulated. Cotton rats are born fully furred and able to move well, and are often weaned at ten days (Meyer and Meyer, 1944:123-124). Voles, on the other hand, are born naked and helpless and are often not weaned for three weeks. It seems, therefore, that extremely wet soil would harm the voles more than it would the cotton rats.

Several instances of cotton rats eating voles, caught in the same live-trap, were noted. There is reason to believe that young voles, unable to leave the nest, are subject to predation by cotton rats. This would accentuate any competitive advantage gained otherwise by the cotton rats.

The population of *Sigmodon* retained its high level, relative to *Microtus*, until February, 1952. In March only one individual was captured and after that none was trapped until August, 1952, when a single subadult male was

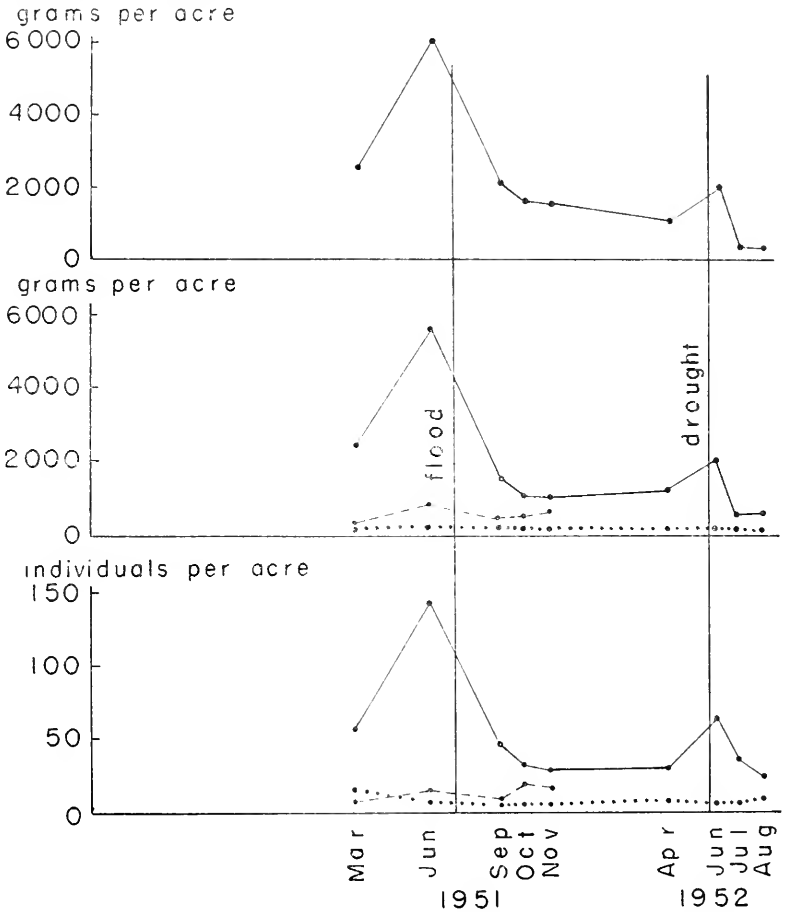


FIG. 18. Variations in density and biomass of three common rodents on Quarry Field. For key, see legend of Fig. 17.

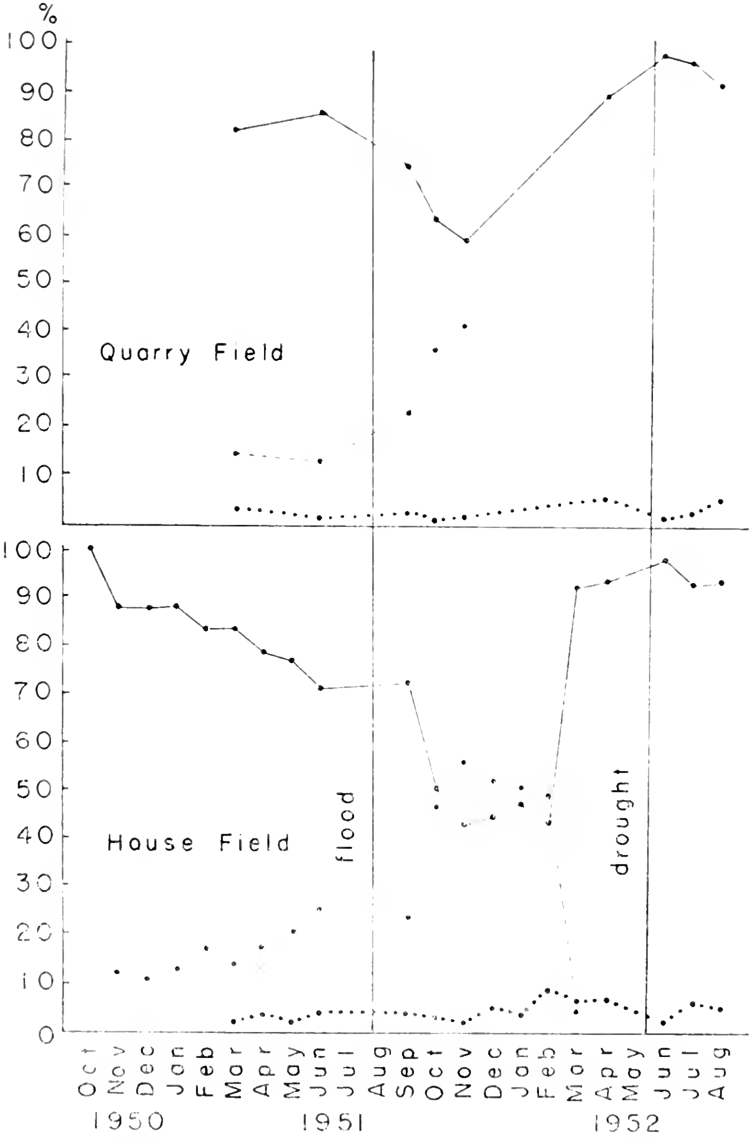


FIG. 19. Changing biomass ratios of three common rodents on House Field and Quarry Field. In late 1951 and early 1952 the cotton rats attained relatively high levels and seemingly caused compensatory decreases in the numbers of voles. The solid line represents *Microtus*, the broken line *Sigmodon*, and the dotted line *Reithrodontomys*.

captured. Early in March, 1952, before the trapping period for the month had begun, the area suffered three successive days of unusually low temperature, with snow, which lay more than six inches deep in places. As suggested by Cockrum (1952:185), such conditions proved detrimental to the cotton rats and, at least to the end of the study period in August, 1952, the population of cotton rats had failed to recover. Perhaps the extremely dry weather which followed the heavy winter mortality delayed the recovery of the population.

These limited data seem to indicate competition between *Sigmodon* and *Microtus* in Kansas. Extremely wet conditions seem to give *Sigmodon* a competitive advantage whereas *Microtus* is better able to survive dry summers and severe winters. However, these relationships need further clarification by an intensive study of the life history of *Sigmodon* in Kansas (especially the more arid western part), including its coactions with the communities it has invaded successfully recently.

The harvest mouse (*Reithrodontomys megalotis*) also was a common inhabitant of the study plots, but this small rodent seemed not to be a serious competitor of the voles, as its food consists almost entirely of seeds (Cockrum, *op. cit.*:165) not usually used by voles. In this study, at least, no conflict over space was apparent. Harvest mice frequently were taken in the runways of voles and even in the same trap with voles. Reithro Field, the part of the Reservation having the heaviest population of the harvest mouse, differed from the habitats that were better for voles in being higher, drier and less densely covered with vegetation. However, during the summer of 1951 when the voles were most abundant, Reithro Field supported a large population of voles. Estimates of population of the harvest mouse were of doubtful validity in summer because it was readily trapped only in winter and early spring. Many individuals marked in late spring were not trapped again until late autumn although presumably they remained on the area. This seasonal variation in trapping success seemed to be a matter of acceptance and refusal of bait (Fitch, 1954:45).

The presence of the wood mouse (*Peromyscus leucopus*) on the study plots indicated an overlapping of habitats. Both House and Quarry Fields were on the ecotone between forest and meadow and a mixture of mammals from both types of habitat occurred. No sign of the homes of the wood mouse was found on the study plots, and on the larger trap line, operated by Fitch, wood mice were captured only near the edge of the woods.

Only six deer mice (*Peromyscus maniculatus*) were taken on the study plots. This small number probably provided an inaccurate index of the association of the deer mouse and the prairie vole, because samples from snap-traps and the data of other workers on the Reservation showed a more common occurrence of the two species together. The deer mice seemed to prefer a sparser vegetation and did not approach so closely to the forest edge as did the voles. It may have been, in part, the presence of *P. leucopus* in the ecotonal region which made it unsuitable for *P. maniculatus*.

Other mammals noted on the study areas were the following: *Didelphis marsupialis, Blarina brevicauda, Scalopus aquaticus, Canis familiaris, Canis latrans, Procyon lotor, Felis domesticus, Sylvilagus floridanus, Microtus pinetorum, Mus musculus* and *Zapus hudsonius*.

SUMMARY AND CONCLUSIONS

In the 23-month period from October, 1950, to August, 1952, the ecology of the prairie vole, *Microtus ochrogaster,* was investigated on the Natural History Reservation of the University of Kansas. In all, 817 voles were captured 2941 times in 13,880 "live-trap days". For some aspects of this study, Dr. Henry S. Fitch, resident investigator on the Reservation, permitted the use of his trapping records. He had captured 1416 voles 5098 times. The total number of live voles used in the study was thus 2233, and they were captured 8039 times. In addition to the voles, I caught 96 cotton rats, 108 harvest mice, 29 wood mice, 2 pine voles and 6 deer mice in live traps. When Fitch's records were used, the live-trapping data covered a thirty-month period and general field data were available from July, 1949, to August, 1952.

Hall and Cockrum (1953:406) stated that probably all microtine rodents fluctuate markedly in numbers. Certainly the populations I studied did so, but the fluctuations were not regularly recurring for *M. ochrogaster* as they seem to be for some species of the genus in more northern life zones. The changes in the density of populations described in this paper can be explained without recourse to cycles of long time-span and literature dealing specifically with *M. ochrogaster* makes no references to such cycles. There is, however, an annual cycle of abundance: greatest density of population occurs in autumn, and the least density in January.

This annual pattern is often, perhaps usually, obscured because of the extreme sensitivity of voles to a variety of changes in their environment. These changes are reflected as variations in reproductive success. In this study, some of these changes were accentuated by the great range in annual precipitation. Annual rainfall was approximately average in 1950 (36.32 inches, 0.92 inches above normal), notably high in 1951 (50.68 inches, 15.28 inches above normal) and notably low in 1952 (23.80 inches, 11.60 inches below normal).

Among the types of environmental modification to which the populations of voles reacted were plant succession, an increase in competition with *Sigmodon,* abnormal rainfall and concentration of predators. In the overgrazed disclimax existing in 1948 when the study areas were reserved, no voles were found because cover was insufficient. After the area was protected a succession of good growing years hastened the recovery of the grasses and the populations of voles reached high levels. In areas where the vegetation approached the climax community, the densities of voles decreased from the levels supported by the immediately preceding seral stages. The higher carrying capacity of these earlier seral stages was probably due to the greater variety of herbaceous vegetation which tended to maintain a more constant supply of young and growing parts of plants which were the preferred food of voles. Later in the period of study the succession from grasses to woody plants on parts of the study areas also affected the population of voles. Not only did the voles withdraw from the advancing edge of the forest, but their density decreased in the meadows as the number of shrubs and other woody plants increased. These influences of the succession of plants on the population density of voles were exerted through changes in cover and in the quality, as well as the quantity, of the food supply.

Whenever voles were in competition with cotton rats, there was a depression in the population levels of voles. Primarily, the competition between the two species is the result of an extensive coincidence of food habits, but competition for space, cover and nesting material is also present. There was one direct coaction between these two species observed. Cotton rats, at least occasionally, ate voles, especially young individuals. In extremely wet weather, as in the summer of 1951, the high survival rate of newborn cotton rats resulted in an increase in their detrimental effect on the population of voles. However, cotton rats proved to be less well adapted to severe cold or drought than were voles.

Heavy rainfall reduced the densities of populations of voles by killing a large percentage of juveniles. During the summer of 1951 the competition of cotton rats further depressed the population level of the voles, but the relative importance of competition with cotton rats and superabundant moisture in effecting the observed reduction in population density is difficult to judge. Perhaps most of the decrease in population which followed the heavy rains was due to competition rather than to weather. Subnormal rainfall, as in 1952, reduced the population of voles by inhibiting reproduction. Presumably because of an altered food supply, reproduction almost ceased during the drought. Utilization of the habitat was further reduced in the summer of 1952 because the voles did not grow so large as they otherwise did.

Predation, as a general rule, does not significantly affect densities of populations, but large numbers of predators concentrating on small areas may rapidly reduce the numbers of prey animals. In the course of my study, such a situation occurred but once, when a group of long-eared owls roosted in the woods adjacent to Quarry Field. The population of voles in that area was probably reduced somewhat as a result of predation by owls.

Population trends in either direction may be reversed suddenly by changes in the factors discussed above. In the fall of 1951, a downward trend in the density of the voles was evident. At this time, populations of cotton rats were increasing rapidly and competition between cotton rats and voles was intensified. In February, 1952, the population of cotton rats was decimated suddenly by a short period of unusually cold weather. The voles were suddenly freed from the stress of competition and the population immediately began to rise. The upward trend began prior to the annual spring increase and was subsequently reinforced by it. In the last part of May, 1952, the upward trend of the population was reversed, as the drought became severe, and the density of the population decreased rapidly. This drop was too sudden and too extreme to be only the normal summer slump. The relatively rapid response of voles to a heavy rain after a dry period, first by increased breeding and later by increases in density, is one more example of abrupt changes in population trends caused by altered environmental conditions.

In the population changes that I observed, no evident "die-off" of adults accompanied even the most drastic reductions in population density. The causative factor directly influences the population either by inhibiting reproduction or by increasing infant and prenatal mortality. The net reduction is due to an inadequate replacement of those voles lost by normal attrition.

Most voles, under natural conditions, live less than one year. Those individuals born in the autumn live longer, as a group, than those born at any other time. Since the heaviest mortality is in young voles, adults which become established in an area may live more than 18 months and, if they are females, may produce more than a dozen litters. No decrease in vigor and fertility was found to accompany aging. A relationship between the condylobasilar length of the skull and the age of a vole was discovered and, with further study, may yield a method of aging voles more accurately than has been possible heretofore. Other characteristics, varying with age, were described. The most reliable indicator of age seemed to be the prominence of the temporal ridges.

Runway systems and burrows are used by groups of voles rather than by individuals. Most of the activity of voles is confined to these runways and an exposed individual is seldom seen. A home range may include several runway systems, and the ranges of individuals overlap extensively. Both home ranges and patterns of runway systems change constantly. Runways seem to be primarily feeding trails, and are extended or abandoned as the voles change their feeding habits. Groups of adult voles using a system of runways seem to have no special relationship. Juveniles tend to stay near their mothers, but as they mature, they shift their ranges and are replaced by other individuals. Males wander more than females, and shift their ranges more often. No intolerance of other voles exists and, in laboratory cages, groups of voles lived together peaceably from the time they are placed together. Crowding does not seem to be harmful directly, therefore, and high densities will develop if food and cover resources permit.

As a prey item, the prairie vole proved to be an important part of the biota of the Reservation. It was eaten frequently by almost all of the larger vertebrate predators on the Reservation and was, seemingly, the most important food item of the long-eared owl. The ability of the prairie vole to maintain high levels of population over relatively broad areas enhances its value as a prey species.

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25-9225

(Continued from inside of front cover)

14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15, 1951.
15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.
17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.
18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-317. November 21, 1952.
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
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27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

***Vol. 6.** (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.
2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.

(Continued on back of cover)

(Continued from inside of back cover)

4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.

5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.

6. Distribution of some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.

7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.

8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.

9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.

10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.

11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.

12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.

13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.

14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.

15. Distribution and systematic position of the pigmy woodrat, Neotoma goldmani. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figs. in text. June 10, 1955.

Index. Pp. 625-651.

Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 2 pls., 26 figs. in text, 17 tables. September 1, 1954.

2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.

4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.

5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.

6. A population study of the prairie vole (Microtus ochrogaster) in Northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figures in text. April 2, 1956.

More numbers will appear in volume 8.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

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UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 8, No. 7, pp. 417-476, 10 figs. in text, 6 tables

June 1, 1956

Temperature Responses in Free-Living Amphibians and Reptiles of Northeastern Kansas

BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
1956

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

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  Index. Pp. 651-681.

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  3. Two new pocket gophers from Wyoming and Colorado. By E. Raymond Hall and H. Gordon Montague. Pp. 25-32. February 28, 1951.
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  5. Comments on the taxonomy and geographic distribution of some North American rabbits. By E. Raymond Hall and Keith R. Kelson. Pp. 49-58. October 1, 1951.
  6. Two new subspecies of Thomomys bottae from New Mexico and Colorado. By Keith R. Kelson. Pp. 59-71, 1 figure in text. October 1, 1951.
  7. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.
  8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.
  9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.
  *10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202. 68 figures in text. December 15, 1951.
  11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.
  12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.
  13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.

(Continued on inside of back cover)

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TEMPERATURE RESPONSES IN FREE-LIVING AMPHIBIANS AND REPTILES OF NORTHEASTERN KANSAS

By

Henry S. Fitch

INTRODUCTION

Climatic Factors and Adaptations to Them.—The field study here reported upon, of temperature in amphibians and reptiles was made chiefly on the University of Kansas Natural History Reservation, 5½ miles north and 1½ miles east of the University campus, in the most northeastern section of land in Douglas County. The general region, being near the geographical center of North America, is characterized by a continental climate, with seasonal extremes of temperature and with frequent sudden changes at all times of the year. Ectothermal animals of terrestrial habits living in such a climate must have developed behavior patterns limiting their activities in time and space to stay within a tolerable temperature range, avoiding the extremes of high and low temperature which occur frequently in the general environment.

Flora (1948) has thoroughly described the climate of Kansas and has presented data for many specific localities in the state, including Lawrence, only a few miles from the site of my study. Data from the Lawrence weather station provide the following items of information: For killing frosts, average latest date in spring is April 10 and average earliest date in autumn is October 23. Average length of the growing season is, hence, 196 days, but in different years it has varied from 221 days to 164 days. Killing frosts have occurred as late as May 6 and as early as September 27. Recorded temperatures have ranged from 45.5° C. to —31.1° (see Table 1).

Table 1.—Monthly Temperatures in Degrees Centigrade, Mean, Extreme Maximum, and Extreme Minimum, for Lawrence, Kansas

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean	-1.2	3.9	6.9	12.8	18.2	23.2	26.1	25.3	21.0	14.6	5.4	.5
Maximum	22.8	28.9	32.7	34.5	38.9	41.6	45.0	45.6	41.1	36.7	29.5	24.4
Minimum	-28.9	-31.1	-19.4	-11.7	-1.1	4.4	10.0	6.7	-.6	-8.9	-15.6	-26.1

Reptiles and amphibians are notably sensitive to temperature. In the Life-zone system developed by C. H. Merriam and his co-workers many kinds were listed as indicators. Relatively few range throughout several life-zones and there are many that are characteristic of a single life-zone. It is characteristic of reptiles that the optimum temperature is only a little below the critical maximum. There is a much wider range between the optimum level and the critical minimum. At progressively lower temperatures the animal becomes increasingly inefficient in its general activity and incapable of essential functions. Chadwick and Rahn (1954:442), for instance, found that the rate of vibration of the tail in a rattling prairie rattlesnake was directly proportional to temperature over the range 37° C. to 5° At the higher temperatures the rate was even higher than the speed of vibration of a hummingbird's wing. At 8° the rate was decreased to less than one-fifth of the maximum.

Environmental temperatures thus control to a large extent the time, place and degree of activity, and impose limitations on the distribution and movements. The Reservation is situated in an area near the margins of the geographic ranges of many species of "cold-blooded" vertebrates. In general, species characteristic of the humid deciduous forests of the eastern United States reach their western limits at approximately this longitude, and others characteristic of the drier regions of the Great Plains and more western states reach their eastern limits in this region. Several species of southern distribution reach their northern limits near the Reservation.

A total of nine species of amphibians and 26 species of reptiles have been recorded from the University of Kansas Natural History Reservation, and at least 24 other species are known to occur within a ten-mile radius. Among these many kinds are animals of extremely diverse habits, and each species is subject to somewhat different limiting factors. Certain species that tend to be ecologically similar show common trends in their responses to temperature and in their ranges of tolerance to temperature.

For each species, environmental temperatures during part of the annual cycle are so low that all activity is inhibited, and so low that death would invariably result if sufficiently insulated hibernation shelters could not be found. For all essential activities, such as breeding, fighting with rivals, feeding, escaping from enemies, travelling, or emerging from shelter, there are separate threshold temperatures. In general, the thresholds are successively lower for each one of the six important activities listed. These thresholds vary but little between individuals of a species, but they differ greatly between species. All practice behavioral thermoregulation to some extent, altering their temperatures from that of the general environment by shifts in position or changes in orientation. The temperature range within which the individual can efficiently perform all or most of its essential functions may be limited to certain situations and to certain times in the annual and daily cycles. In the amphibians moisture requirements impose even more severe restrictions on the time and place and extent of activity. For both amphibians and reptiles, morphological, physiological, and behavioral adaptations are to a large degree designed to overcome or circumvent the limitations imposed by sensitivity to moisture and temperature. Behavioral theromoregulation includes warming by insolation to maintain the body temperature near the optimum level (often much different from that of either the air or the substrate), and the habit of seeking insulated shelters to escape temperatures of the general environment that are either too high or too low.

The main groups of amphibians and reptiles, namely the frogs, turtles, lizards and snakes, differ somewhat in their tolerances of temperature extremes and in their preferred or optimum temperatures. In general, the body temperatures maintained are higher in lizards than in snakes, higher in snakes than in turtles, and probably higher in turtles than in frogs, but there are exceptions to this trend. Those species that habitually frequent open situations and maintain their body temperatures by basking in direct sunlight all have relatively high optima. This group includes nearly half of the species studied. It is noteworthy that species of amphibious habits prefer somewhat lower temperatures than do strictly terrestrial species. Certain other species generally avoid direct sunlight and regulate their body temperatures by resting on the surface of the soil beneath, and in contact with, flat rocks that are warmed by the sun. Species of a third group are nocturnal in their prowling, and ordinarily neither bask in the sunlight nor depend on sunshine-warmed rocks to maintain their body temperatures (except that in cool weather of spring and summer some of them temporarily alternate to daytime activity). Still other species are more or less persistently subterranean, generally remaining beneath the soil surface even when they are active, in contrast with those that emerge for their periods of activity.

METHODS.—The present account is based mainly on observations of reptiles and amphibians under natural conditions, and study of their temperature relationships at different seasons under the special climatic conditions prevailing at this locality. A small amount of experimentation was done, and occasional observations are included on captive individuals under unnatural conditions.

No exhaustive search of the literature concerning temperature relationships of amphibians and reptiles has been made, but a number of earlier publications have been cited that are of special significance or that have pertinent information concerning the species herein discussed, or closely related species.

At the University of Kansas Natural History Reservation field work is carried on nearly every day of the year on a variety of ecological problems. In the course of routine field work I recorded temperatures and responses of amphibians and reptiles living under natural conditions. I usually carried a small Schultheis thermometer of the type first used and described by Bogert (1949:197), and with it recorded body temperatures of the animals and their surroundings.

Many of the amphibians and reptiles examined were in live-traps of different types. For such restrained individuals body temperatures ordinarily were not recorded because the situation was unnatural, but temperature readings from such trapped animals occasionally yielded significant data regarding tolerance of high temperature, or capacity for movement at a temperature below the normal range of activity. At each capture other than those made with traps a temperature reading was taken immediately. In snakes and lizards and the larger amphibians the small thermometer bulb was inserted deeply in the cloaca. In the smaller amphibians, *Acris, Pseudacris* and *Gastrophryne,* the thermometer bulb was used to force the mouth open, and was inserted deeply into the stomach. Approximately 15 seconds were required to obtain a temperature reading. During this time the animal was held down and handled with heavy leather gloves or with several layers of cloth to prevent absorption of heat from the hand of the field worker. In the smallest animals even such handling resulted in disturbance of the delicate temperature equilibrium from the separate heat sources of substrate, air and direct sunlight, so that changes occurred which may have been sufficiently rapid to affect the reading obtained. In the larger animals, body temperatures were found to be much more stable—so that even contact with the bare hand did not affect the temperature appreciably in the short time required to obtain a reading. In each instance the position and activity of the animal was recorded, whether it was in the open or under shelter, and whether it was in shade or sunlight. Air temperature at a height of 40 inches above the point of capture was routinely recorded, and other readings from air and substrate were sometimes taken.

In the present study a total of 1577 body temperatures were obtained for 29 species of amphibians and reptiles. More than 400 readings were obtained from the collared lizard, with smaller numbers for the other kinds, down to a single reading for one of the species. However, for 19 species, body temperatures were obtained in numbers sufficient to show the trends. All temperatures in this report pertain to the Centigrade scale but some were originally recorded in Fahrenheit.

ACCOUNTS OF SPECIES

Bufo americanus.—Smith (1950:81) states that in Kansas "Males have been heard calling as early as March 24 and as late as April 28." At the pond near the Reservation headquarters breeding averages considerably later than these dates would indicate. In 1950 toads were first heard trilling on April 10 at 1 P. M. when the air temperature was near 22.2°. By April 22 the chorus was at its peak. In 1951 the first calling was heard shortly before dusk on April 23 at an air temperature of 21.2°. Calling increased in volume rapidly and was near the peak by April 26. In 1952, a chorus was first heard on April 21, following several warm days with temperatures of approximately 23° and a rain of more than an inch. By April 29 these toads dominated the chorus at the pond. In 1953 and 1954 breeding was delayed by drought. In April 1953 no water was available at the pond or elsewhere on the area. Rain on May 4 and 5 totalled nearly an inch; by May 7 shallow water had collected in the bed of the pond, and that evening several toads were heard trilling. A little more than 1.5 inches of rain fell on May 16 and 17. On the morning of May 18 the pond was filled to overflowing, and there was a great chorus of toads. Air temperature was approximately 17°.

In 1954 the first toad recorded was seen on April 23 at the entrance of a deep crevice in a hilltop rock ledge in early afternoon, perhaps just emerging from hibernation. It was partly in sunshine; the sky had begun to clear only a few minutes before. The toad was alert and wary, and several times when the observer ap-

TABLE 2.—BODY TEMPERATURES OF AMERICAN TOADS IN BREEDING CHORUSES, AND TEMPERATURES OF THEIR SURROUNDINGS.

Date	Toad temperature	Air temperature	Water temperature
May, 6, 1954, 8 P.M.	20°	13°	20°
May 29, 1954, 7:45 P.M.	23.6°	24.5°	24.8°
May 29, 1954, 7:45 P.M.	25.2°	24.5°	24.8°
May 29, 1954, 7:45 P.M.	22.5°	24.5°	24.8°
May 29, 1954, 7:45 P.M.	24.0°	24.5°	24.8°
June, 1, 1954, 9 P.M.	21.4°	14.8°	24.3°
June 1, 1954, 9 P.M.	23.9°	14.8°	24.3°
June 4, 1954	23.5°	14.0°	Not recorded
April 27, 1955	21.7°	27.4°	21.7°

proached, it ran back into the crevice, each time emerging cautiously a few minutes later. The first breeding chorus in 1954 was heard at 8 P. M. on May 6 and in the next few weeks choruses were heard from time to time on warm evenings after heavy rains.

In 1955 the pond was full throughout the season, and availability of water was not a limiting factor. Calling was first heard on April 12 after a rain. A single toad was trilling at 4 P. M. when air temperature was 23.3° and water was 21.5°. By nightfall several more had arrived and joined the first one in a chorus. More rain fell during the night and the weather continued mild. On April 13 calling continued throughout most of the day. All the toads were concentrated in an area about 30 feet in diameter where the water was one to two feet deep. Twenty-one toads including six mated pairs, were caught and marked. Breeding was at its height. Air temperature was 15.8° and water was 21.0°. The afternoon was windy with falling temperature. By 4:30 P. M., when air temperature was 14.3° and water was 19.0°, the chorus had ceased, although in the following hour there were occasional half-hearted attempts at calling by several different individuals. On several subsequent occasions when the toads were heard calling, temperature of both air and water was above 20.0°.

Piatt (1941:264) recorded water temperatures of 23°, 24.5° 25.5°, and 24.5° at times in late April and early May when toads were breeding.

From time to time throughout the season of activity on the Reservation toads were found active in daylight, always at times when the humidity was high. Most of these were small young, which were of course far more numerous than the adults in years of successful reproduction. The records were obtained mostly in hot weather of mid-summer, when the young were most abundant. These records therefore perhaps reflect the upper limit of voluntary tolerance but may not show the entire range or the preferred level, if there is one. The toads were mostly found in damp soil in thick woods. They were usually in heavily shaded places, but did not avoid patches of sunlight. After sunset toads were often found foraging in more open places where none was active in the hotter part of the day. The 72 body temperatures recorded ranged from 32.3° to 17.5° but 57 were in the relatively narrow 26.5° to 31.0°.

In the San Bernardino Mountains of southern California the toads (*B. boreas*) were found to depend on burrows of the golden-mantled ground squirrels and pocket gophers for shelter from both unfavorably high and unfavorably low temperatures in the outside environment (Mullally, 1952:275). Even in spring and autumn when temperatures at night were consistently below freezing the toads were nocturnal in their activity. Their emergence from burrows seemed to be determined by light intensity, but presumably diurnal foraging would expose the animals to the danger of desiccation. Body temperatures of foraging toads on October 19 and 20 varied from 12.0° to 3.0°, the latter being the minimum temperature at which normal activity is possible. At about this temperature the toads retired underground and individuals restrained on the surface froze solid and were killed at approximately —2°. Mullally was able to detect slight temperature differences between the dorsal and ventral parts of the body by taking deep cloacal readings. The dorsal half was slightly more affected by the air temperature, but both dorsal and ventral parts were much nearer to the temperature of the substrate than to the temperature of the air.

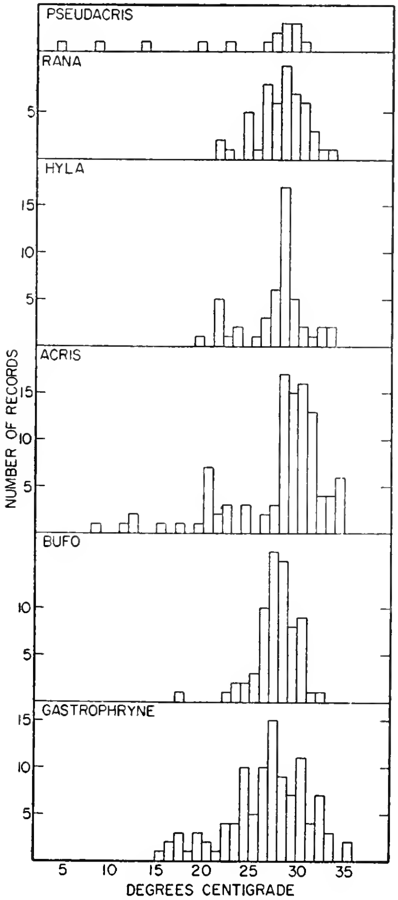

Fig. 1. Body temperatures recorded in five kinds of frogs and toads. For each kind a temperature near 29° seems to be preferred, but the cricket frog and chorus frog are active at relatively low temperatures. For the American toad preferred temperatures and maximum temperatures are somewhat lower than for the others. The ant-eating frog and cricket frog tolerate relatively high levels.

Stuart (1951:221) found that in *Bufo bocourti* of the Guatemalan highlands the critical minimum temperature is slightly below 3.5° while in *B. marinus* of the nearby lowlands, the critical minimum is in the neighborhood of 15°. Critical maximum temperatures similarly differ in these two species, approximately 34° to 35° and 41° to 42°, respectively.

Bufo woodhousei.—The garden toad is rarely found on the reservation and has never been heard in the breeding chorus at the pond. However, it is common on nearby areas where habitat conditions are more favorable. On July 6, 1955, at dusk, a small adult found foraging on a road had a body temperature of 26.5° when air was 25.6°. On July 10, 1955, a young one less than half-grown was found at 10:42 A. M. sitting in sunshine on damp sandy soil of a field near the Kaw River. This toad had a body temperature of 33.7° (air 32.7°), which was higher than was recorded in any individual of *B. americanus*. This suggests that the garden toad is more tolerant of heat.

Acris gryllus.—The cricket frog, usually found near the edge of water, in damp situations, is active over a wide range of temperatures, from slightly above freezing to summer heat. Of the 59 species of amphibians and reptiles in the area of this study, the cricket frog is the only one that is commonly seen in winter. When there are unseasonably warm sunny days, these frogs may be found in small numbers at the edge of the water in the same situations where they are abundant in summer. These seem to be only a small proportion of the total population, and probably are the individuals that have attempted hibernation in the more superficial situations, and as a result have been activated by rising temperatures.

Several hopped into the water when I passed one corner of the pond on the morning of November 14, 1951, while there was still frost on the ground in shaded places. On the morning of December 4, 1954, when the sky was overcast and air temperature was 10.4°, a frog hopped sluggishly over the concrete slab in a gully bottom. On January 16, 1952, when the air temperature was 18.3°, four were flushed along a 50-foot stretch of pond edge. The pond surface at this time was partly covered with ice, although ice had melted along the edges after several days of warm weather. On February 9, 1952, a clear sunny day, many were seen along the edge of the pond at 2:30 P. M. when the air temperature had reached approximately 15.6°. Temperatures had been below freezing for several nights previously.

In March 1955, cricket frogs could be found along the edge of the pond at almost any time when the air temperature was a few degrees above freezing. On March 16 at 11 A. M., when air temperature was only 4.5°, a frog that had been sitting in the sunshine had a body temperature of 20.5°. On the morning of

March 17, when the sky was overcast, and air temperature was 4.6°, a frog crouching on damp soil had a body temperature of 8.3° (approximating that of the substrate). The frog, disturbed by my approach, repeatedly leaped approximately one foot, but its movements were relatively slow and poorly coordinated. This was especially noticeable as it sprawled on the ground with legs extended at the end of a leap. The frog required approximately half a second to withdraw its legs into position for the next leap. As a result it was easily caught. On March 19 at 8:45 A. M., when the sky was overcast, a recently emerged frog was found on mud a few inches from the edge of the water. Air temperature was 4.0°, water was 7.2°, and the mud where the frog was sitting was 6.5°. At my approach the frog hopped clumsily back into the water. No others could be found.

Linsdale (1927:76) wrote of finding several on February 2, 1927, in Doniphan County, northeastern Kansas. "They were in the water above old ice and below a top layer of new ice. All of the frogs were stiff and floating and apparently they were dead." Linsdale observed that these frogs could be found active throughout the winter in the relatively warm water flowing from springs. Blair (1951:178) found cricket frogs active in winter in a spring at a cave entrance.

Three that were kept for several days were in good condition after a cold night, when air temperature in the container had fallen to —1° C. They were almost immobilized, however. When stimulated, they would attempt to jump, but the slow and poorly coordinated contractions of the hind limbs were too weak to drive the body forward.

Despite the cricket frog's winter activity it requires relatively high temperatures to breed. In 1951, calling was first heard at noon on April 27, at a temperature of 31.2°, and on subsequent days the chorus was continued with increasing volume. In 1952, calling was first heard on the afternoon of April 24, at the pond and at a shallow pool in a ditch about 100 yards from it, at an air temperature of 20.6°. In 1953, breeding was delayed, because of drought, and calling was first heard on the evening of May 9, soon after water began to cover the bed of the pond; there had been heavy rains on May 4 and 5. In 1954, calling was first heard on April 27 and again on May 6, a lone individual in each instance. On May 19 desultory calling was heard, and a few more were present by the end of the month. The first big chorus was heard on June 8 at 7:30 P. M. when air temperature was 26.3° and water was 29.3°. In 1955, breeding began much earlier. Calling was first heard on April 10 when air temperature was 22.2° and water temperature was approximately the same. In the following week calling increased; by April 17 there was a sizable chorus and by April 22 it was near the maximum. On May 28, 1955, at an air temperature of 14.6° and water temperature of 19.5° a chorus was heard. In cooler weather the frogs were invariably silent.

In all, 102 body temperatures were recorded, ranging from 8.3° to 34.8°. More than half of the temperatures were within the relatively narrow range 28.0° to 31.7° which seems to be preferred by the frogs. In only a few instances were the frogs' temperatures lower than air temperatures. Usually they were considerably higher. In cool weather the frogs' temperatures often exceeded air temperatures by 10° or more, but in warm weather they basked less and were usually nearer the air temperature. Even on the hottest summer days these frogs have been seen sitting in the sunshine, but not for long periods. One flushed from a shaded spot and caused to jump to a spot exposed to sunshine, but not further disturbed, usually moved to a shaded spot again within two or three minutes. On hot days these frogs avoided overheating by remaining on damp soil that was relatively cool, and also by evaporation of moisture from their skins. The frogs having body temperatures of less than 20° were noticeably slow in their movements and would have been relatively vulnerable to predators. These were mostly individuals that had recently emerged and had not yet had time to adjust their temperatures by basking, or individuals whose basking had been interrupted by cloudiness.

Hyla versicolor.—The tree toad is a relatively late breeder and has not been observed active when temperatures were low. Normally it breeds in the latter half of April. In 1950, earliest calling was not recorded but the tree-toad chorus was near its maximum on April 22 at an air temperature of 30°. In 1951, calling was first heard when temperature had reached approximately 21.2° on the afternoon of April 23, in a gully bottom 100 yards from the pond. On the evening of April 24 at an air temperature of 27° several were calling in the pond. By April 26 the chorus had much increased in volume although the weather had cooled slightly. In 1952, on the humid, cloudy afternoon of April 18, when the temperature was approximately 21.2°, one was heard calling at a distance from water, near the Reservation headquarters. On April

21, at an air temperature of 24° several were heard calling at different places in the woods, and after dark there was a chorus at the pond. In 1953, the first one of the season was heard in the vicinity of headquarters calling late in the afternoon, when humidity was high, after a shower. On May 7 when the temperature had risen to 16° following the rain of May 4 and 5 a tree-toad chorus had started at the pond. On the evening of June 1, 1954, several males that were calling were out of the water near the edges of a small pool when water temperature was 24.2° and air 14.8°. One of these males was found to have a body temperature of 19.2°. The calling tree-toads were flattened against the damp soil, and by conduction from it, evidently were enabled to maintain their body temperatures at levels well above that of the air. In 1955, the first calling was heard at the pond before dark on April 16 when the air temperature had reached 30°. On the evening of April 17 approximately a dozen were calling, and for the following six weeks there was a chorus nightly except on a few occasions when the weather was unseasonably cool. On April 25 several were calling when air temperature was only 16° and water temperature was 18.5° to 20° at the surface. On May 13 several were calling when air temperature was 15.2° and water was 17.4°. On May 15 at 7:30 A. M. two were calling when air temperature was 16.5° and water was 17.5°. On several other nights that same week when temperatures were slightly lower, the choruses were silenced. On the evening of May 29 one was heard to call a few times when water temperature was 17.5° and air temperature was only 10.5°.

In summer when humidity is high tree toads are seen occasionally. At other times they probably keep under cover where they are protected from desiccation. In the summers of 1949, 1950, and 1951 they were often seen at an old rock quarry, and several lived in small holes and niches in the limestone. The rock surface, heated by direct sunlight, was often uncomfortably hot to the touch, but the tree-toads themselves were much cooler. In the hotter and drier summers of 1952, 1953, and 1954 none was found at this quarry.

Most often tree-toads have been seen on foliage of low vegetation. On warm days they have been seen perched on leaves in the sunshine, seeming to suffer no discomfort, as they could have moved into the shade with only short shifts. A total of 48 body temperatures were recorded. For nine recorded from tree-toads that were members of breeding choruses temperatures ranged from 23.7° to

19.7°. For 39 others found away from water in summer, temperatures ranged from 33.7° to 25.7°. The four highest readings, 33.7°, 33.4°, 32.2 and 32° were from individuals that were sitting in sunshine. The greatest number of readings were in the one-degree interval 28° to 29°.

Pseudacris nigrita.—The chorus frog is heard much more often than it is seen, and because of its secretiveness little is known of its habits. It breeds in early spring, soon after thawing provides open water, earlier than any other salientians occurring in the region of this study. Choruses are heard chiefly in March and April, but may be resumed briefly at any time through July, during or after heavy rain.

In 1949, several had begun calling on March 4, at the pond, which still had a thin layer of ice on it. Air temperature was only a few degrees above freezing. By March 21 there was a loud chorus, and the chorus had attained maximum volume by March 25.

In 1950, ice was melting rapidly from the pond on March 4, and when the air temperature had reached 16°, in late afternoon, several chorus frogs were calling. On the following day calling was heard intermittently, and air temperature ranged from 2° to 24°. On March 6, air temperature reached a maximum of 23°, and the calling had become a chorus. The volume of the chorus increased for the next four days, but on March 11 the return of freezing weather silenced the frogs. In the following week calling was resumed, and it reached a peak on March 17. On March 18, although the maximum temperature was only 8.3°, calling was heard occasionally.

In 1951, the first chorus frog was heard in a warm rain on March 1 at an air temperature of 10.5° and another was heard at 7 P. M. on March 4 in the pond bed still containing no water, but damp from recent rains. On March 22 at 2 P. M., with air temperature 23.3°, first chorus of the season was heard at the pond, in which, by then, a small amount of water had collected. By dusk the chorus had increased. This was the first mild day after several weeks of cold weather with temperatures at night usually several degrees below freezing. In succeeding days the chorus rapidly increased in volume.

In 1952, an egg cluster was found in a shallow pool in a gully bottom on February 18. On February 25, at 7.4°, a chorus frog was calling, so slowly that at first I mistook the rasping croak for the rapid drumming of a woodpecker. On February 28 when temperature was a little less than 7°, similar slow croaking was heard. Low temperatures prevailed through the first half of March, and calling was either suppressed altogether or much subdued. On March 16, at 11 A. M. when temperature was 10.5°, several were calling; on March 19, with temperature at 8.9°, there was a steady but somewhat suppressed chorus. On March 20, at 17.8°, the chorus had reached its maximum and was audible from a quarter mile. There was a chorus on March 23, when air temperature was near freezing after a minimum of —7.8° on the previous night.

In 1953, calling was first heard on the afternoon of March 11 when humidity was high and temperature was approximately 12.2°. The calling frogs were at different places in a grassy field and at that time no water was available because of drought. Such sporadic calling was heard from time to time throughout the latter half of March when maximum temperatures ranged from 11° to 20°. On March 30 and 31 more than 1.5 inches of rain fell. By 9 A. M., March 31, the pond bed was covered with a thin sheet of muddy water, and throughout the day frogs were calling from time to time; temperature was approximately 10°. In early April, calling was heard at the pond daily. Usually it was not heard in the morning, until air temperature had risen to at least 4°. On April 1, at 9:30 A. M., a weak chorus had begun when air was 8° and water was 9.3°.

In 1954, as a result of prolonged drought, moisture rather than temperature controlled the time of commencement of the breeding season. Calling was first heard on February 16 at 11 A. M., when air temperature was 6°. After several unseasonably warm days followed by a rain of more than an inch, a lone individual was giving subdued calls, in an open field. At the time, streams and ponds were dry and there was no water available for breeding. On March 7, calling was heard at two different places in open fields when air temperature was approximately 18°. On March 10, as a light rain was falling, at 15.6°, calling was heard in a field. The first breeding chorus was heard on March 25, and approximately an inch of rain had fallen the preceding day. On March 26, the chorus had increased slightly. At 2 P. M. air temperature was 11.8° and the shallow water where the frogs were, warmed by direct sunlight, was 17.6°. On March 28, chorus had increased in volume and the calling frogs were strung out for several hundred feet along seepage pools of the creek bed. There was still scarcely any flow of water. At one shallow pool where dead grass and bulrushes provided abundant shelter, at least six of the frogs were calling within a five-foot radius. I located three males and three clasping pairs. One pair was in the act of spawning, about two inches beneath the surface, and there were many fresh egg clusters. When these observations were made in late afternoon, water temperature was 20.7° and air temperature was slightly higher but a wind had begun to blow from the north. Within an hour air temperature had fallen to 14°. By then the chorus had decreased in volume and some of the frogs had submerged. By noon the next day, air temperature had fallen to —3°. No frogs could be found though search was made on the bottom of the pool. The pool had a thin crust of ice over part of it, and temperature at the bottom was 2°. Temperature remained near freezing with sky overcast, all day on March 30, and there was no activity. On March 31, at 10:35 A. M., slow croaking began in the pool longest exposed to the sun when the ice film had melted and surface water had warmed to 4.9°. Air temperature was 4.5°.

In 1955, there was an ample supply of water. On March 1, the first springlike day of the season, approximately a dozen chorus frogs were calling at the pond when the air temperature was 16.5° and the water was 9.4°. On March 4 at 5 P. M., when air had cooled to 3.3° and water to 7.5°, calling had ceased, with the arrival of a cold front. It was not resumed until March 8 at 10:40 A. M. and at first, calling was slow and sporadic, but 24 hours later it had swelled to a great chorus; air 20.0°, water 7.5°.

In March while the frogs were breeding, air temperatures at night were often somewhat below freezing. The frogs sometimes continued to call even when air temperature was as low as freezing, but the body temperatures of the frogs themselves were many degrees warmer, as they were in the water, nearly submerged. After being silenced by cold the frogs did not resume calling until tem-

TABLE 3.—TEMPERATURE OF AIR AND WATER AT TIMES WHEN CHORUSES OF PSEUDACRIS WERE RESUMED.

Date and time	Air temperature	Water temperature
March 8, 10:40 A.M.	15.5°	12.5°
March 11, 8:35 A.M.	6.5°	10.3°
March 17, 10:30 A.M.	4.6°	8.0°
March 18, 9:30 A.M.	5.8°	8.5°
March 22, 2:30 P.M.	4.8°	3.3° to .3°
March 23, 9:15 A.M.	6.3°	3.4°
March 27, 2:00 P.M.	3.0°	3.0°
March 28, 11:30 A.M.	6.5° to 7.0°	2.8° to 10.5°
March 29, 8:05 A.M.	5.0°	5.7°

peratures were considerably higher than freezing, as shown by the figures in Table 3.

On March 21, 1955, a chorus frog that was nearly torpid was swathed in cotton with a thermometer in its mouth and packed in snow in a battery jar. It was then left overnight in a poorly heated building. In the night the temperature outside reached a low of —14.4°, and was —2° inside the room. On the following morning when the frog was examined, its body temperature was —1.3°, and it was rigid in a twisted position. Obviously some parts of its body, at least, were frozen solid. However, when its foot was stimulated there was a barely perceptible movement. When placed in cold water, this frog soon thawed out and seemed to be unharmed. On another occasion when it was subjected to somewhat lower temperature and frozen solid, it did not revive.

Gastrophryne olivacea.—Ant-eating frogs, near the northernmost limits of the family Microhylidae at the locality of my study, are notably less cold-tolerant than other local salientians. Their season of activity is hence shorter than those of the other local amphibians, and even shorter than for some of the more cold-tolerant reptiles. Earliest dates recorded were: April 25, 1951; April 24, 1952; April 2, 1953; April 22, 1954; April 15, 1955. Late dates of occurrence were October 22, 1949; October 13, 1950; October 7, 1951; and October 27, 1954. In 1952 and 1953, because of drought conditions, none was found after early September. Those found early and late in the season were in moist soil beneath flat rocks, as were most of the others collected, and they were slow and sluggish, not fully active. Hibernation places probably are in deep holes and crevices in rocky places often beneath large boulders. Each spring individuals were found in semi-torpid state beneath large rocks before any were found fully active in the open or caught in traps.

Smith (1950:113) states that breeding occurs from April through September, after rainstorms when the temperature is high. Warmth and heavy rainfall are obviously important factors in determining the time of breeding. However, in the area of the Reservation, breeding only rarely occurs in April or September. In 1955 calling was heard after heavy rains in the second week of May, but otherwise, within the seven-year period of my observations, breeding has been recorded only within the period of late May, June, July and early August. In most years I have heard breeding choruses chiefly in June and July. Several times in late May, 1954, on bright sunny days, numbers of frogs were heard calling, seeming to answer each other, at the site of an old quarry, at a distance from water. These individuals were in damp soil beneath rocks warmed by sunshine. During and after heavy rains on the night of June 1, 1954, there was mass migration to the pond. A chorus was heard on June 2 and for several nights thereafter. On June 4, when the chorus was at its height, soon after dark, air temperature was only 12.8°, but water temperature was 21.4°. In 1955, the frogs were found in abundance in late April. In the week of May 7 to 14, rainfall totalled 2.59 inches. Ordinarily this amount would be ample to cause large scale migration to breeding ponds, but seemingly the low temperature at night, consistently below 13°, and down to 9.4°, prevented them from travelling in any numbers. On May 14, at 1:00 P. M., one was calling at the edge of the pond in sunshine. Temperature of the air was 24.3°, of water 25.7°. For several days afterward a small group was often heard calling at this same place in the afternoon or at dusk, but it ceased as temperatures became lower, soon after dark. Seemingly, the threshold water temperature was approximately 21°. However, on the evening of May 28 one was heard calling briefly when water temperature was 19.5° and air was 14.6°.

Greatest activity occurs on humid or rainy nights when air temperatures are 17° to 25° or even higher. In early September, 1951, because of the successful breeding season increasing the population, and the frequent heavy rains promoting activity, these frogs were caught in large numbers in pitfall traps. In the latter half of the month, however, with nightly temperatures below 15°, few frogs were caught even though moisture conditions remained favorable to them. On October 25 and 27, 1954, four found moving in the open had body temperatures of 17.3°, 17.0°, 16.7° and 16.0°. These individuals were slow in their movements, suggesting that they were near the threshold temperature levels for spontaneous activity.

At a body temperature of 4.3° two captive ant-eating frogs were nearly immobilized. When turned on their backs they often remained indefinitely until stimulated, and then turned over slowly, taking from two to five seconds. Except for these righting movements, the larger frog could not be stimulated to move, and when it was poked, it reacted by merely drawing the legs up closely against the body. The smaller individual could be stimulated to crawl sluggishly for a few inches, but it was unable to hop or to raise its body clear of the substrate. These ant-eating frogs were kept in the same container with several cricket frogs in a poorly heated building in January, 1955. On an exceptionally cold night when air temperature lowered to approximately —1°, both the ant-eating frogs were killed, although they were not frozen solid. However, the cricket frogs with them were unharmed by the low temperature.

Occasionally on warm summer days, ant-eating frogs have been seen scuttling about on the ground but it seemed that in most instances these were individuals flushed from their shelters under rocks by the vibrations of the observer's footsteps as he approached. Ordinarily the frogs do not leave their shelters except under cover of darkness, while rain is falling, or afterward while the soil and vegetation are still wet.

A total of 104 body temperatures were obtained from ant-eating frogs, ranging from 35.7 to 15.5° (see Fig. 1). Seventy-three per cent were within the relatively narrow range 32.6° to 24.0°. There were more records between 27° and 28° than in any other one-degree interval; the median reading was 27.5°. It seems probable that the most preferred temperature is at approximately this level. Approximately 70 per cent of the readings were obtained from frogs that were under rocks in the type of sheltered situations where they usually stayed. For those that were found in the open temperatures ranged from 35.7° to 16.0° and the trend was approximately the same as for the entire sample. The frogs were recorded at air temperatures ranging from 34.0° to 12.3°, but more than half were within a much narrower range, 24.8° to 18.5°.

Rana catesbeiana.—The bullfrog is notably less cold-tolerant in its activities than other salientians that occur locally, and is a late breeder. In 1951, croaking was first heard at the pond on May 8 (air temperature 24.5°) and in 1952 on May 5 (air temperature 31.7°). In 1953, croaking was first heard at 10 A. M. on May 18 when air temperature was 21.5° and water 20.3°. The pond had been dry for many months previously and the single bullfrog heard must have made a long trip overland in the week from May 10-17, when there were almost daily rains and humidity was generally high. In 1955, the first calling was heard on April 22 when air temperature was 26.7° and water was 25.0°.

On October 19, 1952, when air temperature was approximately 20°, numerous bullfrogs of various sizes were seen along the bank at Mud Creek 1¼ miles south of the Reservation. These seemed slow and sluggish in their movements (being screened from sunlight by the steep banks of the creek) and unlike normally active individuals they did not squeal as they jumped into the water.

On November 28, 1951, at 2 P. M., when temperature was near 10°, I flushed two adults on the bank of a shallow pool; they leaped into the water, swam slowly and heavily over the bottom, and hid in mud and debris. On April 1, 1952, the fourth day of maximum temperatures from 20° to 25°, several small bullfrogs were flushed at the edge of the pond. On April 7 adults as well as young were seen at this same place. In 1955, the first bullfrog definitely recorded was seen swimming at the edge of the pond on March 17, at 10:30 A. M., when water temperature was 8.0°.

Bohnsack (1952:114) recorded an instance in which a bullfrog hibernated on land at a distance from water, at the George Reserve in Michigan. The minimum temperature in the hibernation period was —5°. Dormancy terminated when the temperature in the hibernation niche was still below 4°, and when air temperature was 15.6° or less. The same author (1951:238) also observed a green frog (*Rana clamitans*) hibernating in woodland beneath two inches of compact leaf litter. The temperature in the frog's niche was recorded from time to time over periods of weeks, and was sometimes as low as freezing. A maximum-minimum thermometer similarly situated recorded temperatures as low as —8.3°.

On May 30, 1955, shortly before sunrise, when air temperature was 7.5° and water was 16.0°, occasional croaking was heard, but ordinarily when bullfrogs were calling, temperatures were considerably higher, with water 21° or more.

Rana pipiens.—Like the chorus frog and the cricket frog, the leopard frog is active over a wide temperature range. Each spring, its breeding chorus followed soon after that of the chorus frog. On rare occasions individuals were seen active in the winter. Late in the morning of December 12, 1949, one that was half-grown was seen moving among dry leaves in bright sunshine at the top of a deep gully. When it attempted to hop, it was stiff and awkward. It slid and rolled several yards down the steep bank and skidded out onto the frozen surface of a small pool. Minimum temperature had reached —6.6° on the preceding night, but probably this frog was sheltered near the soil surface where it was thawed out by sunshine, even though the air temperature was still slightly below freezing. On December 26, 1954, several were seen, along with cricket frogs, at the edge of the pond in sunshine, when air temperature was 14.4° and water was 10.9°.

On March 3, 1950, the pond was partly frozen over, but rapid thawing occurred that day and the next. Late in the afternoon of

March 4, at air temperature 20.6°, several frogs of this species were seen to leap from the bank into the water at the pond outlet. Calling was not heard until March 22, when several were croaking at the pond along with much larger numbers of chorus frogs. In 1951, the first chorus was heard on March 24. Air temperature was a little above 21° at the time. On January 16, 1952, at 2 P. M., air temperature 18.3°, one flushed at the edge of the pond hopped into the water. On April 1, 1952, and on April 6, 1953, the first leopard frog chorus of each of these seasons was heard. In 1954, none was heard until May 6, although cricket frogs were calling off and on throughout April. Absence of leopard frogs earlier in the spring of 1954 probably was a result of their having been killed by the drought.

On the morning of October 24, 1953, a large adult was found dead and partly dried beside the door of the house. Evidently it had been activated by rain on the night of October 21, but had been unable to find sufficient moisture and had succumbed to drought and frost.

On August 7, 1954, in cloudy weather, when humidity was high and soil was damp, a large adult leopard frog found travelling at a distance from water, near a hilltop ledge, had a body temperature of 28.5°. Air temperature was 27.0°.

In Doniphan County, northeastern Kansas, Linsdale (1927:76) recorded seeing these frogs moving about stiffly on the bottoms of pools which were covered with ice more than half an inch thick. Presumably the body temperatures of these frogs were between 0° and 4°, perhaps nearer the latter figure.

A total of 51 body temperatures were recorded from frogs that were either caught near the edge of the pond or were found travelling far from water at times when the soil was damp and the atmospheric humidity was high. Many of these frogs were recently metamorphosed juveniles. Their temperatures ranged from 33.6° to 21.4°. However, 82 per cent was within the relatively narrow range from 31° to 24°. Those frogs caught near water were nearly always basking in the sunshine and their body temperatures were somewhat higher than air temperatures. The frogs caught travelling at distances from water were mostly found at times when the sky was overcast or were in shaded situations, and they all approximated air temperatures, which were usually between 25° and 30°.

Chelydra serpentina.—Snapping turtles are uncommon on the Reservation. Probably there is no permanently resident population, but wandering individuals make their way up the small intermittent creeks when there is water flowing. In autumn these turtles remain active later than most other reptiles. Several have been seen active in November.

Mr. John M. Legler told me that he caught a large one in Sand Lake, Nicollet County, Minnesota, on March 31, 1953, when the lake was still frozen over except for a 20-foot margin of open water at the shoreline. This turtle was covered with mud and appeared to have just emerged from hibernation. It was sluggish and was caught by hand, but was active enough to snap effectively. On May 5, 1953, Legler caught a snapping turtle that seemed normally active in water that was 9.5°. On November 22, 1953, at Lakeview, Douglas County, Kansas, Legler found two adult snapping turtles moving about an open mud flat in the afternoon. Five others were taken from hibernation sites where they were buried in the mud.

Legler kept several snapping turtles in a large indoor tank on the University of Kansas campus, and he observed sexual activity almost daily when the water was approximately at room temperature. However, when the tank was emptied and cleaned and refilled with cooler fresh water, the turtles became relatively inactive, and sexual activity was not resumed until the water again had warmed to near room temperature.

Terrapene ornata.—In its seasonal schedule the box turtle differs from some other kinds of reptiles in that it emerges late from hibernation and remains active relatively late in the fall. In this respect it resembles most closely the larger kinds of snakes, which are seldom found in any numbers in April but which may remain active along hibernation ledges for much of October, depending on the weather. Earliest recorded dates of activity on the Reservation are: May 8, 1950; May 2, 1951; May 10, 1952; May 31, 1953; April 21, 1954 and May 1, 1955. Evidently emergence is delayed until the ground has been sufficiently moistened and until air temperatures have reached at least 26°. Latest dates of recorded activity are: October 8, 1949; October 5, 1949; September 25, 1950; October 7, 1951; October 24, 1952; October 23, 1953 and October 25, 1954. In hot summer weather these turtles are rarely found, and their activity seems to be largely nocturnal or crepuscular. Ability to endure high temperatures was demonstrated when individuals found crossing roads were captured and confined in the trunk of an automobile, and inadvertently left there after the car had been parked in mid-day sunshine. These turtles survived with no evident ill effects although temperatures of the air and metal around them seemed to be much higher than those that reptiles ordinarily can endure. The box turtle likewise seems to be notably cold-hardy, as individuals have been found active on cool autumn days soon after morning frost had melted. The 55 records of body temperatures for active box turtles under natural conditions indicate a greater range than was found for most other kinds of reptiles from 35.9° to 13.0°. Sixty-two per cent of the total temperature readings were within the six degree range, 30° to 24° with 27° and 28° occurring most frequently. Evidently the optimum level is near these temperatures. Compared with snakes, and especially with lizards, this turtle seems to function efficiently within a relatively wide temperature range. Because of its bulky form and clumsy movement, it is obviously less efficient at making rapid adjustment to external temperatures that are favor-

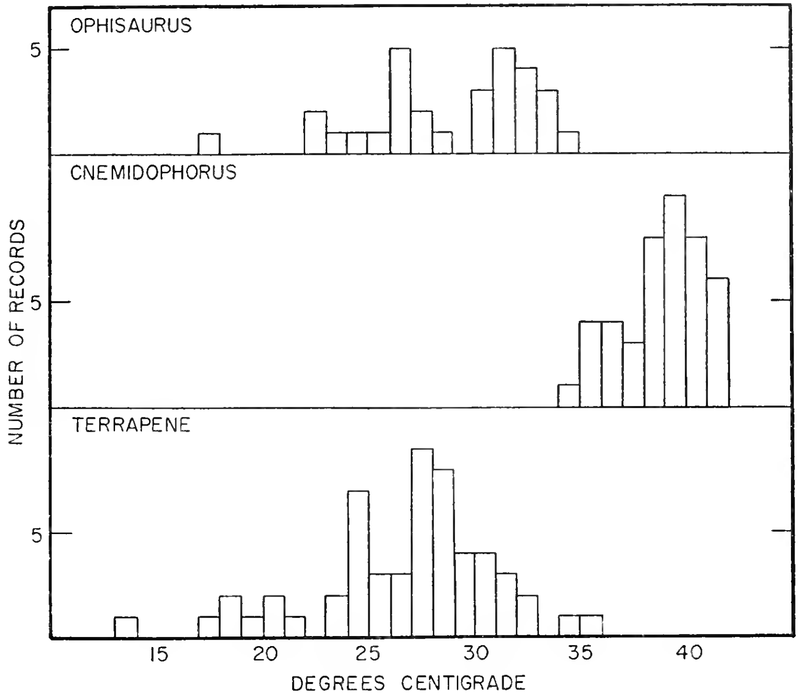

FIG. 2. Body temperatures in three kinds of reptiles of contrasting preferences; in the box turtle range of tolerance is wide and preferred level is low, near 28°; in the glass snake preferred level is several degrees higher and range is narrower; in the racerunner preferred level is notably high, near 40°, and the range is narrow.

able, but it is also less affected by sudden changes to unfavorable extremes of temperature.

Several box turtles were kept by John M. Legler in two outdoor pens, one in a meadow and one in woods. All hibernated within a few inches of the surface. Several turtles equipped with spool trailers in the fall of 1954 were traced to their hibernation sites. All of these had dug into the surface layer of soft soil beneath leaf litter. They tended to choose depressions, as in the bottoms of small gullies where the soil remained moist, and where dry leaves and other wind-blown dead vegetation accumulated, forming an insulating blanket several inches thick above them. Despite this insulating blanket, the temperatures of the hibernating turtles must often have been somewhat below freezing.

Neill (1948:114) noted that in Richmond County, Georgia, large numbers of the common box turtle (*T. c. carolina*) die from freezing in late fall or early spring, when caught away from shelter by sudden cold spells. He believed that more of the turtles were killed by cold than by all other factors combined. This is surprising in view of the relatively mild winter climate in this part of the range. It suggests that winter temperatures too high to permit complete hibernation may constitute a hazard to the animal.

Crotaphytus collaris.—The collared lizard is at the extreme northwestern corner of its geographic range at the locality of this study. The one small colony on the Reservation is at the site of an old quarry, and over a five-year period has shown no tendency to spread from this open rocky habitat. As compared with other reptiles at the same locality, the collared lizard emerges relatively late in spring and retires into hibernation in early autumn.

In a recently published study on the collared lizard's ecology (Fitch, 1956) I have discussed various temperature relationships of the colony observed. The following information is summarized from this earlier report. Earliest dates of activity for the years 1950 through 1955 were April 26, May 12, May 5, April 2, April 6, and April 21. The April 2 record in 1953 was a somewhat premature emergence, and there was no more activity until April 26. The adults are so little in evidence in late August and September, that it seems they may undergo some form of aestivation. Ordinarily hatchlings are in evidence in the early autumn for at least a month after the adults have disappeared. For the years 1949 through 1954 latest dates of occurrence of adults were August 25, September 8, September 6, August 30, September 1, August 27.

Latest recorded dates for young in these same years were September 29, none found in 1950, October 20, October 2, October 10, October 3.

Of 425 recorded body temperatures of collared lizards, 88 per cent were within the six-degree range, 35° to 41°, and more than half (57 per cent) were within the three-degree range from 37° to 40°. By thermoregulatory behavior each individual tends to keep its body temperature near the optimum of approximately 38° even though this may impose severe limitations on its activities. Females tend to maintain slightly higher temperatures than do males. An inhabitant of hot, open situations, the collared lizard prefers a body temperature many degrees higher than the levels preferred by most other amphibians and reptiles of the region; indeed its preferred temperature is at a level higher than most of them will tolerate voluntarily.

Collared lizards were active when air temperature ranged from 13.5° to 36°, but most were found at air temperatures in the eleven-degree range from 23° to 34°. When a collared lizard is active it ordinarily maintains a body temperature well above the air temperature by basking in the sunshine. On exceptionally hot days soil-surface temperatures in sunshine reach at least 60° and probably much higher. Under these conditions the lizards usually stay under shelter, limiting their activity to early morning and late afternoon. At times when they are above ground in the heat of the day they are closely restricted to the shaded spots where temperatures within their range of tolerance prevail.

Several relatively low body-temperatures were recorded from individuals that had recently emerged from shelter and had not yet had time to bask and raise their body temperatures. An adult female was caught on May 28, 1952, at 10:30 A. M. when she was only partly emerged from a rock crevice. Her body was tipped and flattened to receive the maximum amount of sunlight. Her body temperature of 20.7° was the same as the air temperature. On June 2, 1953, at 9:30 A. M. another female was caught in a shaded crevice and her body temperature of 24.8° was also the same as the air temperature. In June, 1953, on several occasions collared lizards were observed in the process of emerging from their night shelters. The two adults present at that time were consistently at least half an hour later than the several yearlings of less than half their bulk. Approximately half an hour might elapse from the time a lizard beginning its emergence came into view deep in the crevice and the time it actually emerged into the open where it received direct sunlight. On June 2, at 8 A. M., air temperature was 19.5° with humidity high and dew on ground vegetation. At 8:20 A. M., yearlings were active. At 8:35 an adult female was seen deep in her crevice, looking out. Nearly ten minutes more had elapsed before she had crawled to the opening and thrust her snout out into the morning sunshine. Further emergence took place by several stages. There was a pause of several minutes with only her head protruding, then she lurched forward so that her shoulders also were exposed to sunshine and basked for several minutes more before the next shift exposing her forebody. Finally she crawled out of the crevice and clung to the vertical rock surface below it, fully exposed to the sunshine. After several seconds she ran slowly and awkwardly to her favorite basking place on a board several yards from the crevice.

Temperature readings below 36° were recorded at times when the lizards were unable to attain the higher levels which they obviously prefer. On May 10, 1952, when the air temperature was only 15.5° one of these lizards, caught as it basked in the sunshine, was found to have a temperature of 31.8°. On April 6, 1953, one was seen basking when the air temperature was only 13.5°. Its body temperature was unknown as it escaped into a crevice. On different occasions when the sky was partly or entirely overcast, preventing insolation, the following temperatures, mostly lower than optimum, were recorded: 36.7°, 36.2°, 36.2°, 36.2°, 35.4°, 35.4°, 35.1°, 35.1°, 34.5°, 33.9°, 33.4°, 33.3°, 32.7°. In some instances when the sky was overcast for a short time the lizards were able to maintain temperature near the preferred level, temporarily at least, by flattening against the warm rocks.

At body temperatures above 40° the lizards usually showed one or more of the following characteristic responses for preventing overheating. (1) They would stand clear of the ground resting on the soles of the forefeet, the heels, and a small part of the tail, thus keeping body contact with the hot substrate to a minimum. (2) They would orient themselves facing the sun, thereby presenting the minimum amount of body surface to insolation, or if heat became too extreme they would seek the shade and finally underground shelter. (3) They would gape, cooling themselves by evaporation from the mucous lining of the mouth. Despite such responses obviously designed to hold down body temperature, the lizard might continue to lie in the bright sunshine when a shift of a few inches to shade could have easily been made.

The precise limits of temperature tolerance were not determined. On one occasion when air temperature was 33.9°, an adult was placed in a hardware cloth wire cone and set in the sun. Within a few minutes its body temperature had reached 44.0° and for the next half hour fluctuated mainly within the range 44.0°-44.5°, but reaching a maximum of 45.3°. The lizard showed signs of discomfort, struggling vigorously to escape from time to time, and panting, with mouth gaping widely, throughout the whole period of the experiment. However, when removed after a half hour of exposure, the lizard showed no ill effects.

An adult male observed at 6° was conspicuously dull colored with none of the usual green showing. When stimulated with a poke or light pinch, he was able to stand erect and hissed at each expiration, but was unable to walk and in a few seconds lapsed into torpor, with his body resting on the ground. When handled he made slow squirming movements, and opened his mouth in threat. One examined at a body temperature of 11.8° was semi-torpid and barely capable of locomotion, dragging himself about for a few inches when stimulated, but soon lapsing into lethargy with his eyes closed. Other more cold-tolerant reptiles and amphibians are relatively active at this temperature level.

Mr. John M. Legler kindly made available his notes on a collared lizard experimentally exposed to low temperatures. When left in a cold room at 0°, the lizard cooled in 14 minutes from 32.7° to 11.5°. When removed, it required 25 minutes to adjust to the air temperature of 25°. Legler noted that at 13.9° the lizard was unable to right itself when placed on its back (although it made feeble attempts to do so). At 17.2° it succeeded in righting itself, and made the first coordinated walking movements, but no locomotion was accomplished. At 18.8° the lizard was able to crawl, and even to jump a short distance when confronted with a barrier.

In desert areas of southern California, Cowles (1941:139) noted that young of the collared lizard, like those of other kinds of lizards, were out later in autumn and earlier in spring than were the adults. He surmised that this early and late seasonal activity was a result of their more favorable surface-mass ratio, permitting them to adjust more rapidly when environmental temperatures were at or above their thresholds of activity. In this region Cowles found an average hibernation temperature of 15.2° in 96 individuals of 14 species. These were mostly at depths of less than 13 inches. Cowles emphasized that the lag in conduction of surface temperatures to relatively deep hibernation sites might delay emergence until a time when conditions had become less favorable.

One of the most characteristic habits of the collared lizard is to dig out a hiding place beneath a large flat boulder. The lizard may tunnel for a foot or more, or it may be able to reach the chamber by squeezing into a crevice without digging a tunnel. The chamber itself is just large enough to accommodate the lizard and to permit it to pivot around to face outward or to make an exit. At night and at times when the outside temperature is either too low or too high, the lizard retires to this shelter, where it is somewhat insulated. These shelters are semipermanent, and serve also as escape shelter from certain enemies. If a person approaches a collared lizard that is active in the open, the lizard usually rushes to its hiding place beneath a boulder, which may be the same boulder it uses for a look-out while it basks. If this sheltering boulder is overturned, the lizard is utterly confused; it may rush from rock to rock in a vain attempt to find another hiding place, and return again and again to the site of its former shelter, running erratically and zig-zagging over the spot in a bewildered manner.

Ophisaurus attentuatus.—The glass snake is only moderately common on the Reservation, and is elusive in its habitat of high grass. Therefore glass snakes were captured in small numbers. Some were caught in wire funnel traps; others were caught by hand, while they were active above ground, and therefore yielded temperature records. Over a five-year period the numbers caught, by months, were as follows: April—1, May—11, June—9, July—4, August—19, September—14, October—10, November—1. Unlike all the other species of lizards occurring locally, the glass snake seems to be as active in late summer and early autumn as it is earlier in the year; most records are in the latter half of the growing season. Earliest and latest records of occurrence in five different years are shown in the following table.

Most body temperatures recorded of glass snakes were well above nearby air temperatures. Half of the 30 were within the 3.1 degree range of 30.6 to 33.7°. Only one had a temperature above this range; the remaining 15 all had lower temperatures and were recorded at relatively low air temperatures or at times when the sky was overcast. Although the habit of basking in the sun was espe-

TABLE 4.—EARLIEST AND LATEST RECORDED DATES OF OCCURRENCE OF GLASS SNAKES ON THE RESERVATION, 1950 TO 1955.

Year	Earliest record	Latest record
1950	May 21	October 3
1951	May 6	October 11
1952	May 14	September 14
1953	May 2	October 19
1954	May 13	November 4
1955	April 24	

cially conspicuous in the glass snake, ordinarily only part of the body was exposed. Because of its slender and elongate form, and the high grass of its habitat, it is easy for the lizard to expose itself to direct sunlight or to gain the protection of shade with relatively minor movements. The lowest body temperature recorded was 17.7°, in a lizard caught while basking on the morning of November 4, 1954, when air temperature was only 8.4°.

Air temperatures at times that glass snakes were caught ranged from 31.6° to 8.4°.

Cnemidophorus sexlineatus.—Of the reptiles on the Reservation, the racerunner requires the most warmth and maintains the highest body temperature. It emerges from hibernation relatively late in spring. Adults retire to dormancy relatively early in autumn, but many hatchlings continue their activity into late September or even early October.

Neill (1948:109) found that in Richmond County, Georgia, this lizard remained abroad in late autumn, but was the last species to emerge in summer. He found it hibernating singly or in twos or threes, in burrows beneath large rocks.

In northeastern Kansas the racerunner is characteristic of xeroseral situations. It is usually found in such open sunny situations as sandbars, roadsides, sandy pastures or cultivated fields. On the Reservation its habitat was limited to several small areas where vegetation was sparse because of poor soil and former disturbance: the old quarry site; gully banks in a barren heavily eroded hilltop field; along a short stretch of rock ledge where the vegetation was subject to grazing and browsing by livestock until 1949; and the dry bottom and banks of an old ditch.

Bogert (1949:199) studied the temperature relationships in this racerunner and several other species of lizards. The lizards were shot and their body temperatures were recorded immediately with a Schultheis thermometer. In twelve *C. sexlineatus* taken in Florida, mean body temperature was 41.0° ± .47, and ranged from 43.0° to 38.5°. Bogert's data indicate that the sexes do not differ significantly in their temperature preferences, and that approximately the same temperatures are maintained at different times of day and at different seasons.

In the course of my field work a total of 45 body temperatures were recorded from racerunners that were active in the open. Most of these were within the range 38.0° to 41.5°, and evidently the most preferred temperature level is between 39° and 40°. Several of the readings obtained are probably well below the level preferred by the lizard and result from the interruption to thermoregulation involved in the chasing and maneuvering that preceded capture of the lizard. In several instances capture was effected when the lizard was chased into a wire funnel trap. Removing it from the trap involved several seconds delay during which it usually lost heat, and this loss was especially rapid if the lizard happened to be a juvenile. Several captures were made at times when the sky was temporarily overcast, preventing maintenance of optimum temperature, so that the lizards had become less active though they had not yet sought shelter. Under such conditions the racerunners depended on concealment rather than speed, and were captured more easily than when they were fully active.

Even when allowance is made for such sources of error, my figures indicate a preferred body temperature some 1.5° lower than that obtained by Bogert in Florida, and only thirteen per cent of those recorded by me equalled or exceeded the preferred temperature of 41.0° that Bogert indicated. I suggest that differences in technique rather than differences in the populations of lizards involved, may be the cause. Possibly some of the lizards stalked by Bogert were caused to run across areas of heated soil or sand before they were shot, and thus raised their body temperatures enough to account for the slight discrepancy in Bogert's figures and my own.

Lygosoma laterale.—The 16 body temperatures recorded in active brown skinks ranged from 33.5° to 22.0°. The average of 28.8° and medians of 28.9° and 28.6° probably approximate the preferred temperature level since 12 of the 16 readings are within the relatively narrow range 30.4° to 27.7°. Air temperatures at the times and places where brown skinks were recorded ranged from 28.5° to 22.8° (down to 14.7° in one).

One of these skinks seen running over a board in thick grass on

March 24, 1950, was the first reptile observed active in the open that spring. On October 22, 1952, when the air temperature was near 21°, one was seen darting through grass and weeds at the edge of woods and this was one of the latest records of reptile activity for the 1952 season. Several times brown skinks were seen active in the open in early morning or just before dusk. The one having a body temperature of 22° was caught on September 23, 1954, at 8:15 A. M. in grass wet with dew, where sunshine had reached only a few minutes before. Air temperature was 14.7°.

Brown skinks are most often seen in leaf litter of the forest floor in heavily shaded situations. The species is probably less inclined to bask in sunlight than is the five-lined skink. Although the number of body temperatures obtained is small, they suggest that the preferred body temperature of the brown skink is somewhat lower than that in the five-lined skink. Such a difference seems plausible in view of the observed habitat differences.

Neill (1948:109) found this species in Richmond County, Georgia, wintering in and about fallen logs, stumps, and rubbish heaps. He noted that it was fairly active even in the coldest weather.

Eumeces fasciatus.—The five-lined skink is by far the most abundant lizard of the Reservation, and the data collected for it are more extensive than for any other reptile or amphibian. Its emergence from hibernation in spring is relatively early; usually some individuals can be found in late March. It becomes active while night temperatures are still below freezing. The ring-necked snake, De Kay's snake and common garter snake are the only other reptiles that normally emerge so early. Earliest records for several years are: March 30, 1949; April 7, 1950; March 24, 1951; March 29, 1952; March 20, 1953; March 31, 1954; March 9, 1955. Five-lined skinks are active in spring at times when air temperatures are obviously far below the optimum level. Absence of a leaf canopy in its deciduous forest habitat, in late March and April permits it to take full advantage of sunshine. After a frosty night, while soil temperature is still only a few degrees above freezing, a skink may be sufficiently warmed by contact with the underside of a flat rock receiving direct sunlight to drag itself into the open. There, orienting itself to absorb the maximum amount of sunlight, it may be able to raise its body temperature to near the optimum level within a few minutes. For example, on the cold and windy but sunny afternoon of March 31, 1954, when air temperature was only 7.5°, an adult male was seen darting along the base of a log, and over it, to escape. Damp soil beneath the edge of the log, from which the skink might have emerged, was 8.4°. The first two found in 1955 were under sunshine-warmed rocks on March 9 and 11 and had normal temperatures of 29.8° and 28.0°, when air temperatures were 25.0° and 17.6°. The total of 215 temperature readings taken (Figs. 3 and 4) did not indicate any one optimum temperature but did indicate a tendency for skinks that are active to maintain their body temperatures within a fairly narrow range. Sixty-eight temperature readings were taken on several skinks in an experimental terrarium with a heated metal plate in one end and a metal plate chilled with ice and "dry ice" in the other end. A

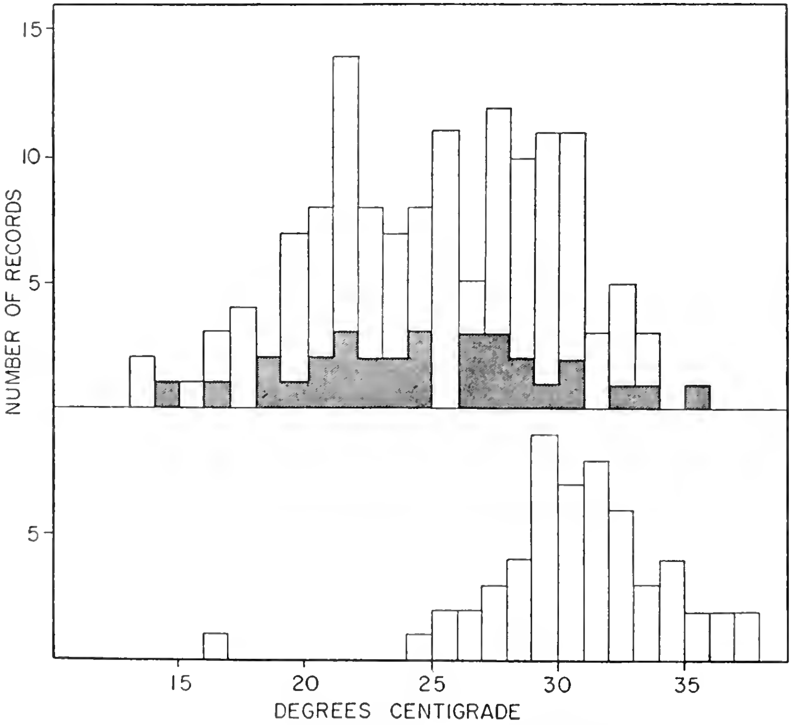

FIG. 3. Body temperatures of five-lined skinks. Lower figure represents individuals caught in the open, which were exercising control over their body temperatures by movement and orientation; all but one are in the relatively narrow range 24° to 37°, and they are especially concentrated in the three-degree range 30° to 33°. The single individual recorded at 17° was newly emerged and had not had time to attain the preferred temperature level. Upper figure represents individuals found under shelter, and these were found where the temperature range was wider than it was in the open. Shaded records represent females in nests, and they do not deviate from the general trend.

narrow strip of screen across the middle of the terrarium was the only place where the lizards could stop for more than a few seconds without raising or lowering their body temperatures much beyond the levels that were comfortable to them. Under these conditions most of the lizards' behavior was motivated by attempts to regulate their body temperatures. Wandering onto either end of the experimental terrarium a lizard soon had its temperature raised or lowered beyond the optimum range and hastened to make readjustment by shifting its position. The skinks tended to cluster in the middle strip, and even there tended to reorient themselves frequently to make minor adjustments. Because of the extremes of temperature to which the skinks were subjected in the terrarium, body temperatures were recorded over a wider range (21.6° to 38.2°) than in those found under natural conditions; nevertheless, more than half of the total were within the four-degree range, 32° to 36°. Within each of the one-degree intervals 32° to 33° and 33° to 34°, ten readings were recorded—more than for any other one-degree inter-

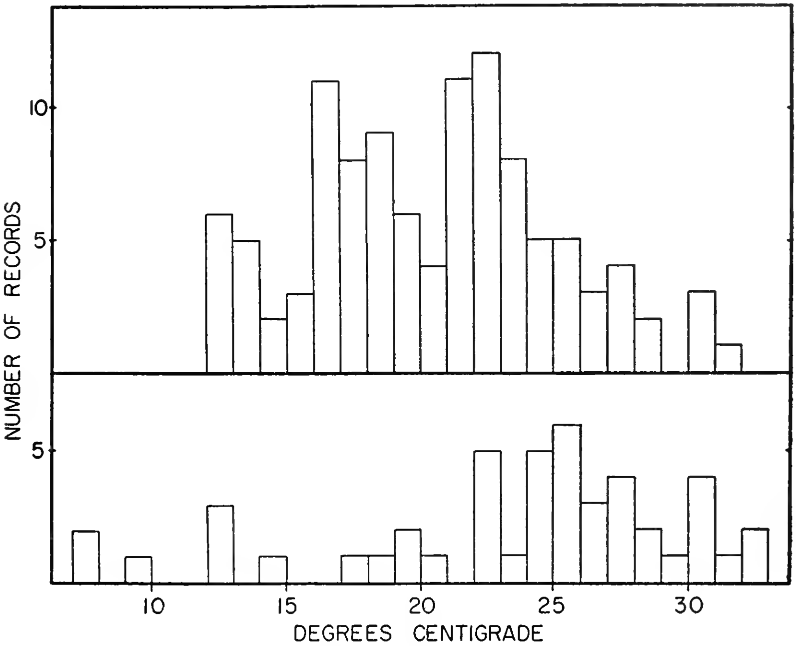

Fig. 4. Air temperatures recorded at times of captures of five-lined skinks; lower figure represents records for the skinks caught in the open, and upper figure represents records for those found under sheltering objects. On the average the active individuals were found at somewhat higher temperatures.

vals, and it seems that the optimum temperature for the five-lined skink falls within this two-degree range. At higher temperatures successively fewer readings were recorded, up to 38.2°, which probably is near the maximum that the skink will voluntarily tolerate. Nine readings were recorded for the one degree interval, 28° to 29°, and 5 for the interval, 29° to 30°. These 14 readings perhaps represent the lower temperature level which these skinks will tolerate without vigorous attempt to readjust the body temperature upward. There were only three readings below 28°.

Fifty-six five-lined skinks that were captured while they were active under natural conditions had temperatures that ranged from 16.6°-37.0°. More than half of the total were within the four-degree range from 29°-33°. Average and maximum temperatures of those skinks captured in the open were somewhat below those of the skinks tested in the experimental terrarium. In such small lizards temperature change is extremely rapid. Most of the skinks found in the open maneuvered to escape and could not be caught immediately. Probably, therefore, they lost some heat in the short interval between interruption of normal thermoregulatory behavior when the collector approached, and the time when the temperature reading was taken immediately after capture. Body temperature recorded in each one of the 41 skinks was somewhat above the air temperature. Usually the disparity was only a few degrees, but sometimes was greater, as shown by the following body temperatures with air temperatures in parentheses: May 2, adult ♂ 27.5° (12.6°); May 2, adult ♂ 30.5° (12.6°); May 10, adult ♂ 30.2° (12.4°); May 28, adult ♀ 32.3° (17.0°).

Temperatures were recorded for 105 other five-lined skinks that were found under rocks. Of this group, 29 were adult females in their nests. The temperatures of the females ranged from 15.9° to 34.0°. Gravid and incubating females are able to exercise limited thermoregulation without leaving their nest burrows, but this varies according to the nest site chosen. By pressing against the underside of the overlying flat rock at a time when it is heated by direct sunlight, the female is able to absorb some of its warmth and when the air and soil are well below optimum temperatures, females are frequently found in this position. In hot weather when the overlying rock is overheated the female withdraws to the deeper portion of the nest cavity, and may interpose a layer of moist earth between the cavity and the rock, and she may deepen the burrow by transferring soil from the bottom to the top of the cavity until it has been displaced downward two or three inches.

Of the 76 skinks, other than nesting females, that were found under rocks, some doubtless had interrupted activity in the open and retreated, unseen, to shelter as I approached. Having been under cover for only a few seconds in some instances, these individuals had high body temperatures like those of skinks caught in the open. Some of the other skinks probably were active but were staying beneath sheltering objects where they were found. In some instances, soil and air temperatures were so high that basking was unnecessary, and in other instances, when the sky was overcast and the air was cool the shelters were the warmest situations that could be found even though they were a little below the optimum. Nearly half of the 76 skinks found under rocks had body temperatures within the six-degree range from 20° up to 26°. Observations on captive skinks have shown that they are fully active at temperatures in the lower twenties, although they are somewhat slower than at optimum temperatures. They tend to confine their activities to well sheltered situations at the lower temperatures. A few individuals, those found at temperatures below 16°, were nearly immobilized and were incapable of effective efforts to escape or defend themselves. Such individuals are, however, able to move about clumsily and take advantage of any available heat source to activate themselves.

Eumeces obsoletus.—The Great Plains skink seems to resemble the five-lined skink in optimum body temperature level and range of tolerance. However, the two species differ in general habits. On the Reservation there is partial habitat segregation, *E. fasciatus* occurring chiefly in woodland and *E. obsoletus* occurring chiefly in rocky and brushy grassland situations. Over its range as a whole, *E. obsoletus* occurs in a drier and warmer climate than that in the region occupied by *E. fasciatus*. *E. obsoletus* is more secretive in habits and is less often seen in the open. The habit of basking in sunlight to raise the body temperature is conspicuous in *E. fasciatus*, but I have rarely observed *E. obsoletus* basking. Usually it does not emerge until temperature of the air and surface of the soil in the shade are near its optimum level. A total of 17 temperature readings were taken on individuals that were active in the open; ten of these readings were on skinks in confinement under conditions permitting them to regulate their body temperatures. Of the 17 readings, 12 were in the four-degree range from 32° to 36°, indicating that the optimum temperature level is within this range. Thirty temperature readings were taken on Great Plains skinks caught under flat rocks. The trend paralleled that of the more extensive data for the five-lined skink. Temperatures ranged from 17° to 36°.

Each year these skinks have been first found on or near the Reservation in April, several weeks later, on the average, than the earliest emerging individuals of *E. fasciatus.* For the years 1949 through 1955, earliest dates of recorded occurrences were on the 24th, 7th, 19th, 2nd, 2nd, 18th, and 17th of April, respectively (Fitch, 1955: 65). Occasional individuals may emerge somewhat earlier. Mr. W. R. Brecheisen found one basking in sunshine on the afternoon of March 14, 1955, in Anderson County two miles east and one and one-half miles north of Colony, Kansas.

On June 19, 1955, a female was found with a clutch of 18 recently laid eggs under a large flat rock. The female's temperature was 31.0° and nearby moist soil in which the eggs were lying was 29.5° when air temperatures was only 24.4°.

Eumeces septentrionalis.—Only two individuals of the prairie skink have been found on the Reservation, one in 1951 and one in 1953. The habitat is becoming less favorable as rank vegetation closes in on formerly open areas. There are well established colonies of the prairie skink within a few miles of the Reservation in heavily grazed pastureland.

Four body temperatures of prairie skinks were obtained in the course of my field work. Each skink was under a flat rock exposed to sunshine. One in Wabaunsee County, Kansas on May 12, 1952 had a temperature of 24.4° (air 17.5°). Others found approximately five miles south of Oskaloosa, Jefferson County, had body temperatures of: 32.0°, 29.6° and 28.0° (air 29.0°). The temperatures of these prairie skinks approximated those of five-lined skinks caught at the same time and place, and it seems that preferences are similar in the two species, although the prairie skink is less inclined to venture away from cover.

Natrix sipedon.—These partly aquatic snakes probably have lower body temperatures than most other reptiles. An adult male was caught in a funnel trap on November 8, 1954, after most other reptiles had retired into hibernation. A juvenile was found under a rock on April 16, 1953, at 4 P. M., before most kinds of reptiles had emerged. It had a body temperature of 16.0° (air 16.6°). The body temperature was obtained twice when it was found active in the open. On September 3, 1953, at 8 A. M., it was 24.0° (air 22.5°) and on September 10, 1953, at 5 P. M., it was 28.3° (air 32.5°). One found under a rock at the edge of Tonganoxie State Lake on

May 22, 1955, had a body temperature of 29.5° when the air was 23.2°.

Carpenter (1953:78) found these water snakes hibernating in a vole burrow at depths of six to fifteen inches, and in a crayfish burrow at 22 inches submerged in water at 2°. Lueth (1941:130-131) found that snakes of this species and garter snakes could survive temperatures as low as 1.5° (one was kept for 56 days at this temperature) but that they were killed at —2°. Lueth concluded that a temperature of approximately 25° is most nearly optimum for these and other small snakes. He found that mortality was heavy at temperatures of 36.5° to 43°.

Storeria dekayi.—DeKay's snake is not common on the Reservation, and partly because of its secretive habits, it is seldom seen. Several have been recorded in March, before most kinds of other reptiles were active, suggesting that it is one of the most cold-hardy species. On March 26, 1951, I found a pair coiled together among dry leaves. Most of those seen moving about in the open were active in early morning or near dusk. The only body temperature obtained was 23.8° in one found under a rock when air temperature was 16.2°. Air temperatures were 26.7° and 21.5° at times when two others were found in the open but not in sunshine.

Bailey (1948:215) found a communal hibernation den of this species in Iowa, at the time the snakes were emerging in late March, 1939. The den consisted of a labyrinth of small subterranean galleries to a depth of 18 inches, in soil composed of mixed sand and clay in a site almost free of vegetation. Besides more than a dozen found active on the surface and a dozen found alive in the galleries, more than 20 dead snakes were found in various stages of decomposition, in the galleries. All of the dead snakes were within ten inches of the surface. The winter had been comparatively mild, and Bailey was led to suggest that such mortality during hibernation may be an important limiting factor to populations of snakes.

Thamnophis sirtalis.—This garter snake is notable for ranging farther north than any other North American reptile, and obviously it is extremely cold-hardy. Its hardiness was emphasized by trapping experience along hibernation ledges where it was caught in some numbers along with several other kinds of snakes. Seemingly the garter snakes did not arrive at the ledges in numbers until the catches of copperheads and blue-racers had passed their peaks and most of these snakes had retired into hibernation (Fig. 8). On November 3, 1951, after three freezing nights, with minimum down to —4°, I made a final check of the traps and found: 1 blue-racer, 1 copperhead (dead) and 7 garter snakes (1 dead). On March 25, 1953, a juvenal garter snake found under a rock had a recently ingested frog (*Pseudacris*) in its stomach. Probably this individual had become active on March 20 or 21 when maximum air temperatures were 27.2° and 23.3°, respectively. On other days air temperatures never rose above 19.5° and night temperatures were usually below freezing.

On April 11, 1953, a large adult garter snake was found entangled in a wire bird trap when the air temperature was approximately 4.5°. Although almost helpless at this temperature, the snake showed fight, facing me with mouth wide open, and swaying. It was actually unable to strike. When released and stimulated, it made feeble attempts to crawl, but was scarcely able to progress. It had probably become entangled days earlier when maximum air temperature had reached 21.5°.

One garter snake was found active on February 24, 1954, the earliest recorded date of activity for any kind of reptile. When found at 4 P. M., basking in subdued sunshine on a bank, its body temperature was 24.0° C. and air temperature was 25.0°. Another was found active on February 28, 1951. Latest recorded dates of activity for the years 1949 to 1954 were: November 11, November 14, November 13, November 12, November 13, and November 13.

Body temperatures obtained from a subadult male found twice in the open in the fall of 1953, were, on October 30 at 11:30 A. M., 20.0° (air 18.6°), and on November 13, at noon, 17.1° (air 18.2°).

From the observations of Bailey (1949:238), Criddle (1937:142) and Carpenter (1953:78) it is known that these snakes may survive temperatures as low as —2°, that there is considerable mortality in hibernation, and that the snakes may choose hibernation sites that are dry, damp, or under water.

Tropidoclonion lineatum.—The lined snake has not yet been found on the University of Kansas Natural History Reservation, and probably it does not occur there. It has been found in a rocky prairie habitat at several localities within a few miles of the Reservation. On April 18, 1954, and April 17, 1955, approximately five miles southwest of McLouth, Jefferson County, Kansas, these snakes were found beneath rocks exposed to sunshine, while air temperature was between 24° and 29°. For eleven lined snakes body temperature averaged 30.5° ± .53.

Hamilton (1947:209) found seven hibernating individuals at depths of six to eight inches in a plot of 1200 square feet of black gumbo soil at Dallas, Texas.

Diadophis punctatus.—Ring-necked snakes are found each year in large numbers in late March, April and May, but despite their great abundance, they are seldom seen in hot dry weather of summer. Most of those seen were in hiding places beneath flat rocks, and they are to a large extent nocturnal in their activity. However, on various occasions they have been seen moving about, in the open on cool days after summer rains, or in early autumn. Evidently temperature is the most important factor in controlling their activity. Ordinarily these snakes avoid direct sunlight, but several found on cool autumn days were basking in sunshine and had body temperatures much exceeding nearby air temperatures. Few other reptiles are found active at such low air temperatures. Obviously small size is an advantage permitting rapid increase in body temperature when sunshine is available. In spring, ring-necked snakes are rarely seen basking in direct sunlight but warm themselves by contact with the undersides of flat rocks heated by the sun. In these situations they are less affected by sudden drops in air temperature than they would be on the surface.

A total of 145 body temperatures were recorded, mostly from ring-necked snakes found under flat rocks, since relatively few were found moving in the open. From the concentration of records (40) in the two-degree interval 29° to 27°, it seems evident that this is approximately the optimum temperature. Approximately 71 per cent of the records were within the range 25° to 31°. Ring-necked snakes were found at air temperatures ranging from 31° to 7°, but all those found at air temperatures below 16.2° were under cover.

In the winter of 1954-1955, two adult ring-necked snakes and a brown snake were kept in a battery jar in a laboratory building. There was loose soil in the bottom of the jar, and a small water can was kept in it. The snakes spent nearly all their time in this water can. On the morning of January 27, after an overnight low, outside, of —17.7°, the water in the can was partly frozen and was of slushy consistency. The surface had not frozen solid, probably because of the snakes' movements. When removed from the can, the snakes were helpless and incapable of locomotion. They made extremely slow and poorly co-ordinated writhing movements. Both the ring-necked snakes died on the following day but the brown snake survived.

In Richmond County, Georgia, Neill found this species to be a gregarious hibernator. He found groups of as many as a dozen together, often in the pulpy wood of decaying logs. In northeastern

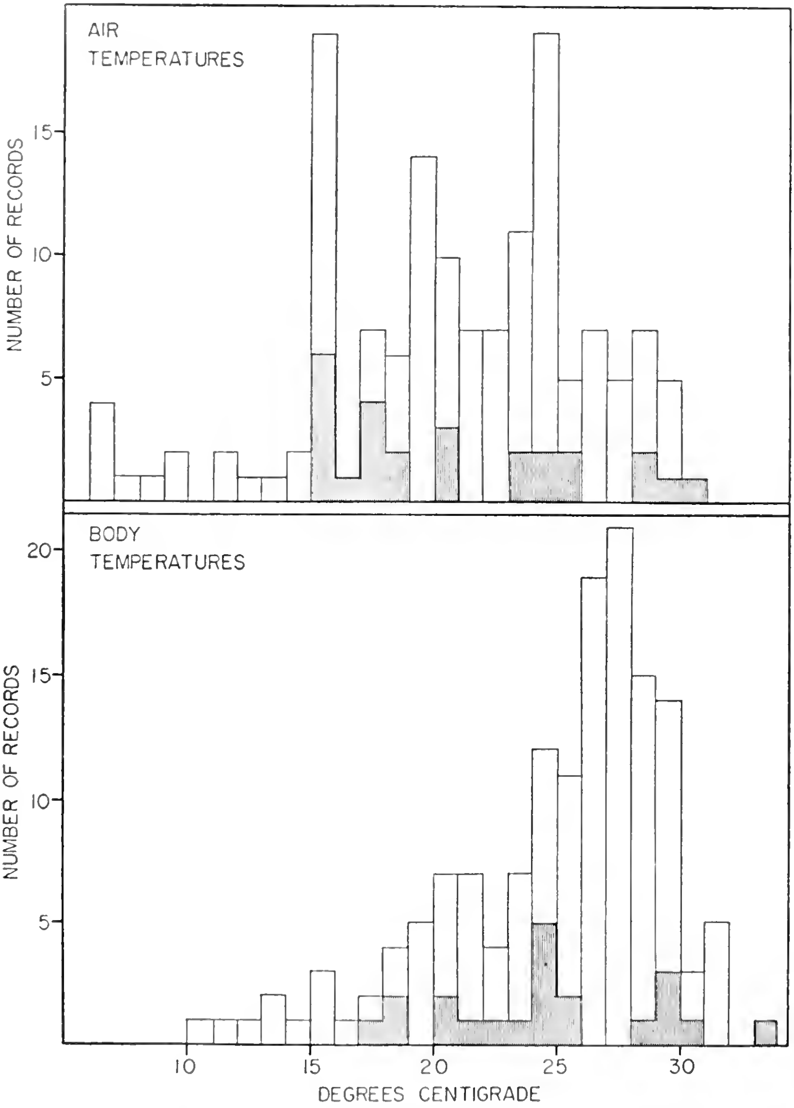

FIG. 5. Body temperatures (lower) and air temperatures (upper) for the ring-necked snake; shaded portions represent records for those found in the open, others were found under shelter. Preferred temperatures seem to be in the narrow range 27° to 29°, and over a wide range of air temperatures most of the snakes had body temperatures in or near this range.

Kansas the species probably does not hibernate in decaying wood, but rather in the soil in deep burrows and crevices. It is somewhat gregarious at all seasons, but especially in March and April, when several or many may be found together under flat rocks. Such groups are to be found in the first warm spell before there is opportunity for surface travel, and it seems likely that the snakes have hibernated in the same underground cavity. These aggregations occur even along rock outcrops when potential hibernating sites are numerous. On April 15, 1955, a group of 19 were caught and marked at a rock pile where aggregations had been noticed each spring since 1949. In the following week none could be found at the rock pile, but several of the marked individuals were found at scattered points within a 100-foot radius.

Grizzell (1949:231) found an adult hibernating, solitarily, at a depth of 32 inches in sandy loam on the Patuxent Research Refuge in Maryland.

Carphophis amoenus.—On the Reservation the worm snake has never been observed moving about above ground. Presumably movement above ground takes place mainly or entirely at night. Occasional wandering is demonstrated by captures in pitfalls and funnel traps, and appearance beneath isolated rocks or other objects. For the years 1951, 1952, 1953, and 1954 combined numbers of worm snakes recorded for each month of the season of activity were as follows: March—7; April—23; May—41; June—27; July—10; August—7; September—10; October—1. Nearly all those recorded were found under rocks. Temperature was recorded for 20 of the worm snakes taken. Excluding one outstandingly low body temperature, these averaged 26.4° and ranged from 31.7° to 19.0°. Average and maximum body temperatures were markedly lower than those of any other kind of reptile studied. In most years worm snakes are rarely found in hot weather of July, August and September. Evidently they shun high temperatures by retreating deep underground. In the summer of 1951, which was characterized by unusually heavy precipitation and subnormal temperatures, these snakes were found much more frequently than usual.

On March 29, 1954, a worm snake was found beneath a flat rock about one foot in diameter. There had been several days of mild weather, preceding arrival of a cold front, and at mid-day when the snake was found, air temperature was —3°, with a light snow falling. The temperature of the snake itself and of the soil around it, was approximately 3.5°. When the snake was placed on the ground in the open beside the rock, it made feeble attempts to drag itself back to shelter at first, but within a few seconds it was chilled to immobility.

Worm snakes perhaps emerge from hibernation earlier, on the average, than any other kind of snake, although ring-necked snakes, because of their much greater abundance, are often found earlier. A worm snake found under a board on February 27, 1951, was the first reptile found that year. One found on March 19, 1953, was likewise the earliest recorded reptile of the season. However, in 1952, none was found until April 17. Worm snakes found in spring under flat rocks, recently emerged from hibernation shelter, often were associated with ring-necked snakes. Evidently these two diminutive snakes form interspecific denning aggregations.

In Maryland, Grizzell (1949:231) dug out a hibernating worm snake on February 8, 1949, at a depth of 24 inches in sandy loam. At a temperature of 9.5° the snake was fairly active and capable of normal wriggling movements.

Haldea valeriae.—Few brown snakes have been found on the Reservation. A juvenile found under a flat rock on the afternoon of October 6, 1954, had a body temperature of 23.5° and air temperature was 21.7°. One found at the same time and place as the lined snakes mentioned above had a body temperature of 31.0° and air was 24.2°. It also was beneath a flat rock.

The individual found on October 6 and kept through the winter proved to be more resistant to cold than were ring-necked snakes that were kept with it. Both ring-necked snakes died after a cold night when particles of ice formed in the water can where all three snakes usually stayed. The brown snake survived, however. On the morning of February 11, the water in the container was found to have frozen solid with the snake inside it. Nevertheless, when the ice melted, this snake still appeared to be unharmed, and it survived. At temperatures near freezing it usually stayed in the water, floating with its body nearly vertical. Occasionally its snout protruded. At temperatures a few degrees above freezing it sometimes emerged from the water can and crawled about the container or coiled beneath the water can. Neill (1948:112) noted that in Georgia wintering individuals are usually in moist soil.

Coluber constrictor.—Of the 16 species of snakes occurring locally, the blue-racer is the one that is most active and most characteristic of open situations. It is sometimes found at temperatures above those which most of the other local species of snakes will tolerate. Also, it is moderately cold-tolerant. Emerging relatively early in spring, and remaining active late in fall, it has a longer season of activity than most other reptiles of this region.

A total of 29 blue-racers were caught while they were active in the open, and their body temperatures ranged from 37.4° to 20.6°, with an average of 30.9° and median of 30.7°. More than half were in the 3.4° range from 29.3° to 32.7°. Air temperatures ranged from 32.3° to 17.5° for this group. For five other blue-racers that were found under rocks, body temperatures ranged from 30.5° to 15.5°.

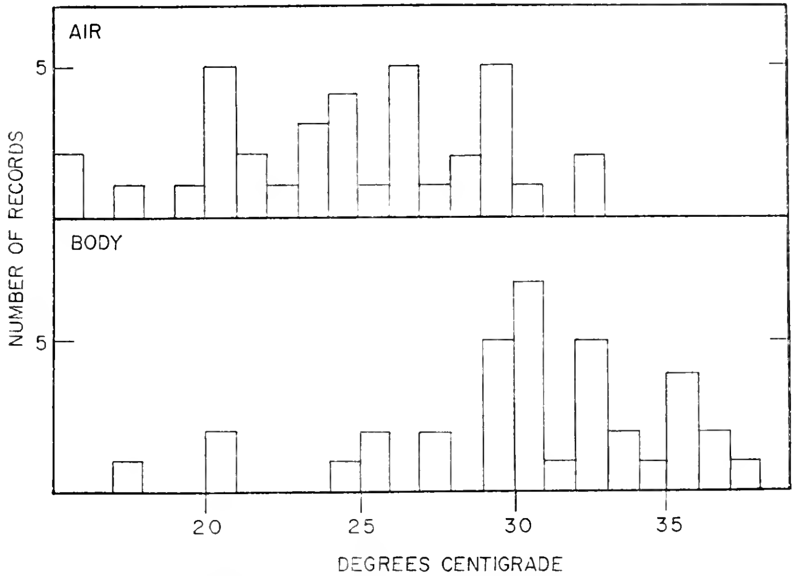

FIG. 6. Body temperatures (lower) and air temperatures (upper) of blue-racers. These snakes bask in sunshine and are usually warmer than the air. Preferred temperatures seem to be in the range 25° to 36°.

Earliest recorded dates of activity were in April each year, for 1950 through 1955 the 16th, 19th, 23rd, 8th, 20th and 15th. Latest recorded dates of activity were October 28, 1949, November 4, 1950, November 13, 1951, and November 12 in 1952, 1953, and 1954.

Several of the individuals to which these records pertain were juveniles. The hatchlings appear in late summer, and grow rapidly in the many weeks before retirement into hibernation, and they constitute a substantial part of the hibernating population. Because of their relatively high surface-volume ratio, they are able to make more rapid adjustment than adults to environmental temperatures, and therefore tend to continue their activity somewhat longer in the fall and resume it somewhat earlier in the spring.

Although blue-racers were caught in large numbers, most of them were obtained in funnel traps, and therefore did not yield significant data concerning temperature. Because of their speed and elusiveness, these snakes usually escaped when attempt was made to catch them by hand. One caught on October 5, 1951, had the lowest body temperature, of only 20.0°; it was basking on a rock when the sky was partly overcast, and probably it was unable to attain a higher temperature under these conditions. On October 22, 1952, one having a low temperature of 25.8°, was caught basking late in the afternoon when the sun was low, and its temperature was only a little above the air temperature.

Figure 8 shows the numbers of copperheads, blue-racers, and garter snakes caught along hibernation ledges in autumn. Blue-racers are scarce along these ledges in summer, having dispersed to open fields. The figures show that, on the average, the racers are most abundant along the ledges about mid-October, some two weeks later than the peak for copperheads, but nearly two weeks earlier than the peak for garter snakes.

Neill (1948:110) noted that in Georgia this racer continues its activity until late in autumn and is one of the first snakes to emerge in spring (February or March). He found it hibernating in tunnels left by the decay of pine roots.

Cohen (1948:137) saw racers emerging from a hibernation den near Baltimore, Maryland, on April 6, 8 and 10 at air temperatures of 12.5° and 18.5°.

Owens (1949:90) found eight blue-racers and seven pilot black snakes hibernating together in an old cistern. These snakes were submerged, two to eight inches beneath the surface, with their tails anchored in crevices. When discovered, on March 3, 1949, the snakes were not completely dormant, but would occasionally thrust their snouts above the surface to breathe. Owens determined that this cistern was usually dry in winter, so the snakes probably were not hibernating underwater by choice. However, like the garter snakes and water snakes found by Carpenter in a crayfish burrow, they were tolerant of submergence. Schroder (1950:1-2) on February 11, 1950, found several blue-racers hibernating at depths of 36 inches and 42 inches in a mammal den in a sand dune area of western Illinois. The snakes were intertwined in compact masses, five adult blue-racers with two adult bull snakes in one mass and two juvenal racers with two juvenal bull snakes in another. Their temperatures were 6.7° and the frost line was 8¼ inches beneath the soil surface.

Elaphe obsoleta.—The pilot black snake is the largest kind of reptile on the Reservation. It is neither especially late nor especially early in its average time of emergence and retirement. Earliest recorded dates on the Reservation are: April 12, 1950; April 15, 1951; April 26, 1952; April 8, 1953 (two found under rocks; not found in open until April 21); April 8, 1954; April 18, 1955. Late records are: October 22, 1949; October 31, 1950; November 2, 1951; October 16, 1952; October 23, 1953; October 25, 1954. These snakes are only moderately common on the Reservation, but as they are not especially swift or elusive, most of those seen in the open were caught and their temperatures recorded.

A total of 53 body temperatures were recorded from pilot black snakes found in the open. These temperatures ranged from 38.0° to 18.2°, but 73 per cent were within the relatively narrow range from 30.7° to 24.0°. Air temperatures ranged from 31.5° to 15.2°.

The highest body temperature recorded for any snake in the present study was one of 38° in a pilot black snake found under a

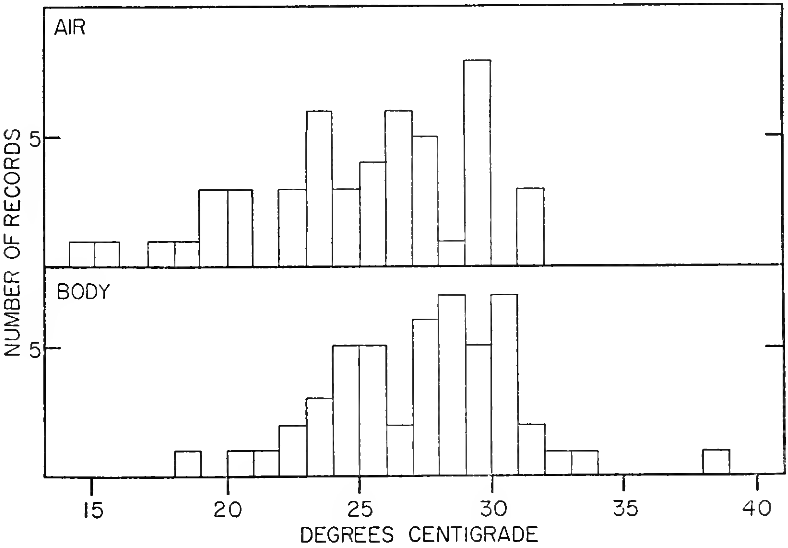

FIG. 7. Body temperatures (lower) and air temperatures (upper) of pilot black snakes; the body temperatures average only a little higher, as basking is less characteristic of this snake than of some other kinds of reptiles. Body temperatures within the range 24° to 31° seem to be preferred.

piece of scrap metal exposed to sunshine on the afternoon of May 10, 1953, when the air temperature was only 16°. The second highest reading recorded for a pilot black snake was 33.5° on June 27, 1952, in a female lying partly in the sunshine while in the act of egg-laying in a rotten stump.

In spring and autumn, pilot black snakes have been found basking in the sunshine on numerous occasions. In summer they usually avoid exposure to sunshine except in early morning or late afternoon. Their woodland habitat exercises a moderating effect on the temperature, and the snakes may be active either by day or by night.

Figure 8 shows that pilot black snakes, on the average, were most active along hibernation ledges in the last week of September, coinciding with the peak of activity in copperheads. Only one pilot black snake was recorded in November in any of the six years over which the study extended. This species seems to retire to dormancy somewhat earlier than does the copperhead, blue-racer or garter snake.

Pituophis catenifer.—Bull snakes are seldom found on the Reservation, and most of those caught have been taken in funnel traps along rock ledges where they come to hibernate in fall. Body temperatures were obtained for only eight individuals. For a large adult male found on September 19, 1951, coiled under a flat rock, temperature was 26.7° and air temperature was 21.1°. For a half-grown male, on April 27, 1953, at 2:30 P. M., body temperature was 29.5°, air temperature 22.1°. In an adult female found lying partly in sunshine on October 7, 1951, body temperature was 19.5° and air temperature was 15.3°. An adult female found crawling in the sunshine on April 24, 1954, had a temperature of 32.4°.

Two found on June 5 and 6, 1954, had temperatures of 25.2° and 29.0°, and each was several degrees warmer than the air, and a pair found basking together on May 10, 1953 had body temperatures of 31.5° and 30.5° when air was only 15.2°.

Lampropeltis.—Three species of king snakes occur on the Reservation, *L. calligaster*, *L. getulus*, and *L. triangulum*, but all of them are rare. Therefore but little was learned concerning their temperature relationships. Body temperatures for five *triangulum* were 31.7°, 26.8°, 26.3°, 23.7° and 22.3°, and for two *calligaster*, 33.0° and 30.4°. No conclusions can be drawn until a larger sample is available.

Agkistrodon contortrix.—The coupperhead is common on the Reservation, but is not often seen in the open, as it is largely nocturnal in habits and has effective concealing coloration. In early spring and in fall, when night temperatures are unfavorably low, it is more likely to be out in daylight. Most of the copperheads found in the open were taken either near the beginning or the end of the active season or else were out in early morning or at dusk, or on cool, cloudy days. Each year copperheads have been first found in April; in the years 1950 through 1955 they were found on the 15th, 24th, 23rd, 8th, 25th and 20th, respectively. Latest dates of occurrence recorded were: October 27, 1949; November 14, 1950; November 20, 1951; November 12, 1952; October 31, 1953; November 16, 1954.

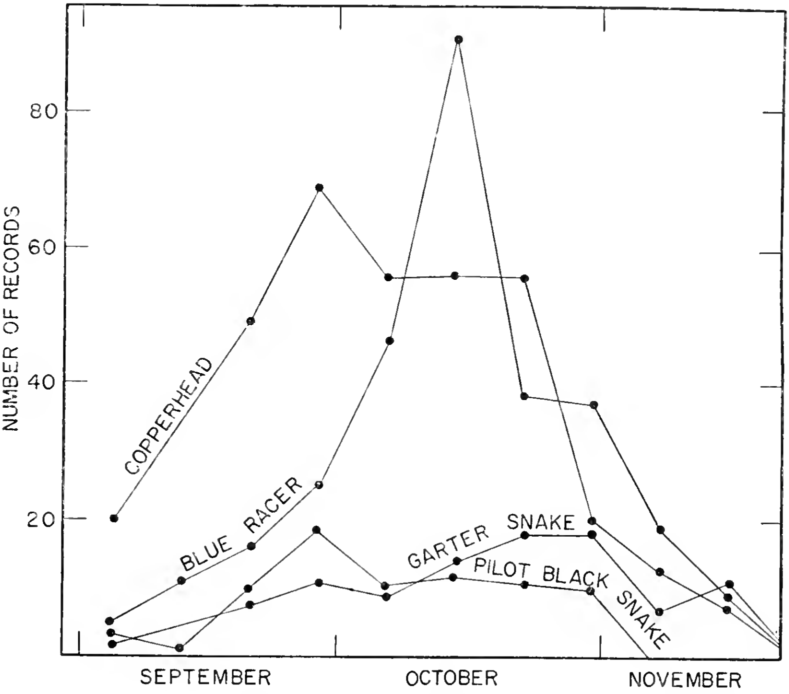

FIG. 8. Numbers of copperheads, blue-racers, garter snakes and pilot black snakes caught along hibernation ledges in autumn. For each species the numbers represent five-year totals (1949 through 1954) grouped in one-week intervals. The copperhead and pilot black snake are present in greatest numbers in late September, while the blue-racer is most in evidence some three weeks later, and the garter snake does not attain maximum numbers until the end of October.

A total of fifty-nine body temperatures was obtained from copperheads found under natural conditions. These ranged from 34.5° to 15.5°. For the 39 found active in the open, body temperatures ranged from 34.5° to 17.5°, and air temperatures ranged from 32.4° to 11.7°; two-thirds were within the range 30.0° to 25.5°, which seems to be preferred. For 20 others found under flat rocks or similar shelter, body temperatures ranged from 30.5° to 15.5° and air temperatures ranged from 30.7° to 21.7°.

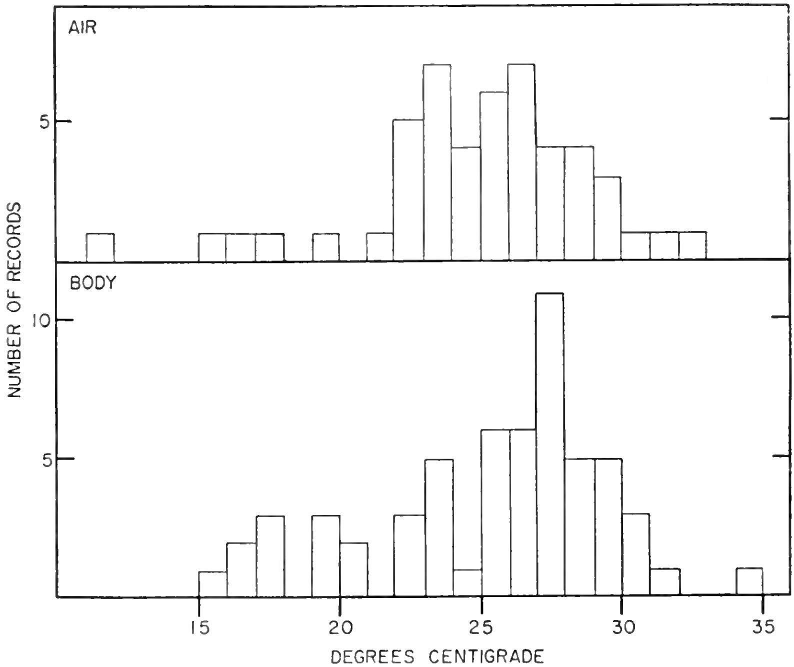

FIG. 9. Body temperatures (lower) and air temperatures (upper) at captures of the copperhead. Preferred temperatures seem to be in the range 25° to 30°, and the air temperatures average only a little lower than the body temperatures, since these snakes bask in sunlight only occasionally.

On October 18, 1951, four copperheads found in funnel traps, which they had entered in warmer weather of preceding days, were released at a temperature of approximately 10°, and their reactions were observed. When dumped on the ground in the open, they lay in semi-torpor, without attempting to escape or defend themselves. When handled, however, they struggled in a slow-motion version of the usual defense and escape behavior, squirming and throwing the body into a kink, and attempting to bite. When released at the edge of a rock crevice, each withdrew into the shelter almost immediately, disappearing within a few seconds.

Crotalus horridus.—Timber rattlesnakes are rare on the Reservation, and but few observations on their temperature relationships have been obtained. Too few individuals were obtained to provide a clear idea of the seasonal schedule. The 35 captures of rattlesnakes recorded on the Reservation over a six-year period were distributed by months as follows: April—1; May—1; June—2; July —none; August—1; September—6; October—21; November—3. It is noteworthy that more captures were recorded in October than in the remainder of the year. The relatively large numbers found in autumn can be accounted for in part by the fact that these usually nocturnal snakes become diurnal with the advent of cool autumn weather, and hence are more frequently encountered. A more important factor is the relative abundance of the newborn young in autumn before their numbers have been reduced by various mortality factors. For example, 19 of the 21 captures recorded in October involved juveniles.

Body temperatures recorded were: 22.2° on April 25, 1952; 21.2° on May 17, 1951; 27.2° on June 2, 1953; 31.7° on August 8, 1951; and 27.0° on October 16, 1954. Although the timber rattlesnake resembles the copperhead in habitat preference, it tends to be more closely confined to rock ledge situations in warmer and drier surroundings. Most of the timber rattlesnakes seen in the open were coiled basking in sunshine, while relatively few copperheads were found basking. Optimum body temperature for this rattlesnake probably is several degrees higher than the optimum for the copperhead.

DISCUSSION AND CONCLUSIONS

SEASONAL SCHEDULES.—For the eight frogs and toads, two turtles, seven lizards, and fifteen snakes occurring on the University of Kansas Natural History Reservation, records of activity indicate that there is an annual cycle regulated to a large extent by temperature. For every month in the year some activity has been recorded in amphibians, and reptiles have been observed active in every month except December and January. In late November, December, January, February, and early March, however, activity is at low ebb. In February the chorus frog may become active and may even breed, and after unseasonably warm weather an occasional five-lined skink or ring-necked snake may be found at the soil surface beneath sheltering objects, and the garter snake may be found basking in the open. Late March and early April is the peak of breeding activity for the chorus frog and leopard frog. Also in late March, several of the smaller kinds of reptiles—the five-lined skink, ring-necked snake, worm snake, DeKay's snake and garter snake may be found commonly at the soil surface beneath sheltering objects, and on warmer days the five-lined skink and DeKay's snake have been found in the open. In early April, if weather is especially mild, there may be breeding choruses of the common toad and tree-toad, which by the end of the month are on the wane. The five-lined skink, ring-necked snake, worm snake, DeKay's snake, and garter snake are active. Other species including all the larger kinds of snakes and lizards may be found under sheltering objects in late April, but some of them are not found in the open until mid-May or even later.

The smaller kinds of amphibians and reptiles become active earlier in the season than larger kinds do. Likewise, the young, of certain species at least, typically emerge earlier in the season than the adults do. In this climate, characterized by abrupt seasonal and daily changes in temperature, small size confers a distinct advantage in permitting rapid rise in body temperature by contact with warmed soil, rock or air, until the threshold of activity is attained. In consequence, the smaller kinds are active for as much as a month in spring before the larger kinds have emerged; their young benefit from a longer growing season. For the larger species of snakes the season of activity is terminated abruptly by the onset of freezing or near-freezing weather. For lizards and smaller kinds of snakes, however, activity tapers off more gradually; for some it ends before the onset of cool autumn weather, and temperature evidently is not the controlling factor. Adults of several common lizards, the five-lined skink, Great Plains skink, collared lizard, and racerunner, are not often seen after mid-August.

These poikilotherms seem to be somewhat more regular in their annual cycles than the weather itself, suggesting an inherent rhythm. Weather deviating from the seasonal norm in spring may hasten or delay emergence from hibernation in the five-lined skink (Fitch, 1954:44 and 83) and the collared lizard (Fitch, 1956: 223); the changed times of emergence may have far reaching effects on the time of breeding and the fortunes of the annual brood of young produced. In other species similar changes from year to year occur, but they have been less thoroughly studied.

Dates of recorded emergence each year did not show close correlation with recorded air temperatures, either for the day of the record or for the preceding period. Many factors other than the maximum daily air temperature affect the temperature and reactions of the hibernating animal, stimulating it to activity and emergence. Air movement, as in high winds serves to hasten the warming of the insulating soil layer. Moisture content of the soil alters its conductivity, and if the soil is damp on warm days emergence may be hastened. Insolation increases as the season advances and the angle of the sun becomes greater, with sunlight more concentrated. As a result, animals under shelter near the soil surface may be warmed to activity even on days when air temperature remains relatively low. In the well insulated hibernation shelter, the timing of the dormant animal's ultimate activation is affected by all temperatures from the time of the beginning upward trend in early spring. Periods of moderately warm days and mild nights may be more effective in bringing the animal's temperature up to the threshold of activity than a single unseasonably hot day early in the season.

Examination of the recorded emergence dates when reptiles and amphibians were first found each year, over a five-year period, discloses that in almost every instance the temperature on the supposed emergence date had been exceeded at some time earlier in the spring. In some instances a species failed to appear in an unseasonably warm spell early in the spring but it did appear weeks later in relatively cool weather. The recorded emergence dates are in most cases only approximations. Some may be based on single individuals prematurely emerged. In other instances recorded emergence dates lag somewhat behind the time of actual emergence, because of occasional interruptions in the field work, and because some of the scarcer and more secretive species are not seen regularly even when they are active.

OPTIMUM TEMPERATURES AND RANGES OF ACTIVITY.—Cowles and Bogert (1944:277) have recognized several ecologically important temperatures. For each species there is a normal activity range, limited by the voluntary minimum tolerance and the voluntary maximum tolerance. At either of these two thresholds the animal ordinarily seeks shelter. Beyond this normal range are the critical minimum and the critical maximum—thresholds at which effective locomotion is prevented and the animal is helpless. The lethal minimum and maximum are those threshold temperatures at which even short exposure produces irreparable damage, and death results.

In my study nearly all the temperatures recorded were within the normal activity range, since under natural conditions individuals rarely allow themselves to become overheated beyond it. In its hibernation shelter the animal is nearly always below the normal activity range. Throughout most of the winter, it is below the critical minimum. There is evidence that hibernation temperatures falling below the lethal minimum are a major cause of mortality in amphibians and reptiles.

For many species, including the American toad, cricket frog, tree-toad, ant-eating frog, leopard frog, ornate box turtle, brown skink, ring-necked snake, pilot black snake, and perhaps the common water snake, DeKay's snake, common garter snake and brown snake, the preferred temperature level seems to be in the neighborhood of 28° to 29°. Definite preference for lower temperature is indicated for only two species, both snakes. The copperhead's preference seems to be between 27° and 28°, and the worm snake's, which is the lowest of all, seems to be between 26° and 27°. For the glass snake and the lined snake preference between 29° and 32° are indicated, and 31° is approximately the optimum level for the blue-racer. For the five-lined skink, Great Plains skink, and prairie skink the preferred levels are in the lower thirties. For the collared lizard the preferred level is approximately 38°. For the racerunner the preferred level is the highest— 39° to 40°. For snakes and turtles, and especially for frogs and toads, preferences are less clear-cut than for lizards. Preferred temperatures are usually in the upper part of the normal activity range, and may be only a few degrees below the critical maximum.

Amphibians and reptiles are most easily found in a period of weeks in spring after the advent of mild weather. At this season deeper layers of soil are still unfavorably cool. Even at the surface the soil is usually somewhat below the optimum for most species, except when it is in sunshine. Flat rocks provide the most preferred type of shelter at this time. The animals lie on the soil with their dorsal surfaces in contact with the rock's undersurface, absorbing warmth from it, and often maintaining temperatures well above those of both the air and the soil.

At times when the rock becomes overheated by sunshine, or chilled on cool nights, the animal withdraws from contact with it, wriggling into loose soil until embedded, or retiring to greater depth in a crevice or burrow. Few of the species are efficient burrowers even when fully active. Most of them depend on natural cavities or those excavated by rodents, moles, shrews or insects, at most merely enlarging or altering the cavities somewhat. The six-lined racerunner, Great Plains skink, and ornate box turtle dig better than other kinds, but even these species depend to a large extent upon holes that are already available. Even those species that are nocturnal or secretive during summer are much in evidence at the surface in spring.

Basking in sunshine is characteristic of the cricket frog, tree-toad, bullfrog, leopard frog, collared lizard, glass snake, racerunner, five-lined skink and blue-racer. This group includes the species that have the highest body temperatures. Utilization of rocks for shelter and thermoregulation by contact with sunshine-warmed rocks rather than by direct sunlight, are characteristic of the ant-eating frog, Great Plains skink, prairie skink, DeKay's snake, lined snake, brown snake, ring-necked snake, worm snake, and the three species of king snakes. Preferred temperatures average somewhat lower for this group than for the species that habitually bask in the sunshine. Other species do not regularly bask in direct sunlight nor depend on sunshine warmed rocks for shelter, and most of them are persistently subterranean or nocturnal. In these species body temperature ordinarily approximates the temperature of the soil or the air surrounding the animal. This group includes the species characterized by lowest body temperatures—the American toad, chorus frog, worm snake, prairie rat snake, bull snake, copperhead, and timber rattlesnake.

Cowles and Bogert (1947), Bogert (1949) and others have demonstrated the importance of behavioral thermoregulation in the lives of reptiles, and the differences in preferred body temperatures. Optimum temperature level is a trait of phylogenetic significance, since species within a genus and even genera in the same family tend to be similar in this regard while groups that are only distantly related may differ correspondingly in their preferred temperature levels.

Amphibians, in general, are able to function efficiently at lower temperatures than those at which reptiles are active. Amphibians also are active over a wider temperature range than reptiles are, but they are easily injured by lack of moisture and high temperature. Bogert's study (1952) of several species of plethodont salamanders in Virginia, indicated that these amphibians exercise no control over the thermal levels of their bodies, but approximate the temperatures of their normal surroundings, especially those of the substrate. Bogert found most of the species investigated (genera *Desmog-*

nathus, Plethodon, Eurycea) living under moist conditions where substrate temperatures were between 15° and 18°. Turtles also are tolerant of wide temperature range, and are capable of functioning at relatively low temperatures. The lizards are characterized by maintenance of high body temperature within a relatively narrow range through behavioral thermoregulation, during the time of activity. The skinks, and the anguid, iguanid, and teiid lizards maintain successively higher body temperatures. The six-lined racerunner, with a body temperature exceeded only by birds is characterized by high metabolism, with rapid and almost continuous movements during its periods of activity. Therefore, it competes on more nearly equal terms than do most reptiles with the homoiothermal birds and mammals, when environmental temperatures permit, but it is penalized in habitat restriction and short growing season. To a somewhat lesser degree the same statements apply to the collared lizard, the only iguanid of the area. It prefers a temperature range high compared with those of most reptiles, but a little lower than that of the racerunner.

In snakes the optimum temperatures average lower than those in lizards, and the range of activity is somewhat wider. The preferred temperature differs according to habits and habitat of the particular kind of snake and is successively higher in: those that are of secretive habits or nocturnal, or both; those that occur in a forest habitat, and those that frequent open situations and are diurnal.

DORMANCY.—All of the amphibians and reptiles at the locality of this study spend a large part of the annual cycle in torpid condition, but the duration of dormancy differs widely among the different kinds. The season of activity is perhaps shortest in the collared lizard, which may be in evidence for as little as one-third of the year—from May through August. The cricket frog perhaps having the longest season of activity, is regularly active from early March through much of November, and intermittently through the winter in warm spells. Its dormacy may amount to less than one-fourth of the annual cycle.

The differences in time of emergence and retirement between the many local species are due to (1) differences in choice of hibernation sites, as in depth, type of soil, and slope exposure; (2) differences in response to low temperatures. Some kinds of amphibians and reptiles are capable of limited activity even at temperatures near freezing, and are able to respond to such cues as favorable temperature gradients by moving toward the soil surface, while others are still totally immobilized, requiring much higher temperatures to become active.

There are numerous reports in the literature concerning observations or experiments on the hibernation of amphibians and reptiles. Vernberg (1953) enclosed 57 salamanders (*Plethodon cinereus* and *Eurycea bislineata*) in screen cages three feet square in their natural habitat. In one enclosure excavated on February 22, 70 per cent of the salamanders were at depths of 11 to 15 inches where the soil was in the temperature range 3° to 4°. After the advent of warmer weather the soil in the second enclosure was excavated and 80 per cent of the salamanders were within four inches of the soil surface. In laboratory experiments Vernberg found that the sala-

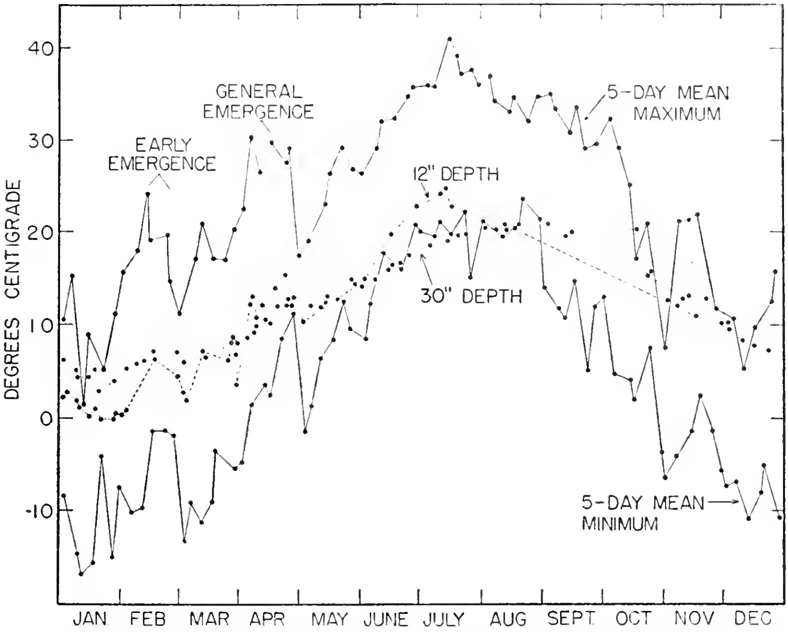

FIG. 10. Records of temperature at the University of Kansas Natural History Reservation in 1954. Upper line shows means of five-day maxima and lower line shows means of five-day minima. Actual temperature readings through the year, underground, at two sites selected as typical hibernation shelters—one 30 inches beneath the surface in a crevice of a hilltop rock outcrop, and the other twelve inches beneath the surface in bottomland—are shown. At the 30-inch depth temperatures were always moderate, well above freezing in winter and remaining somewhat below the normal activity ranges of most reptiles even in the hottest weather of summer. At the 12-inch depth fluctuations were greater, but temperatures were much more stable than those at the surface.

manders kept at low temperatures would respond to a soil temperature gradient by burrowing in the direction of higher temperatures.

Carpenter (1953) noticed recently born garter snakes about an ant hill in October. He built an enclosure about the opening and recorded emergence dates of 75 small snakes of six different species over the period March 27 to May 31. The following February 25 he excavated the ant hill and recovered 77 amphibians and reptiles of 11 species. Temperatures ranged from 3° to 10° in these hibernating animals. Two of the four snakes in the upper five inches of soil where temperature was 1° (and probably had been much colder) were dead. Carpenter found a second aggregation of 16 snakes of six different species in the burrow of a vole (*Microtus pennsylvanicus*) at depths of six to 15 inches. In a third hibernaculum, a crayfish burrow filled with water, Carpenter found five adult common garter snakes at depths of three to 27 inches. The range of emergence dates was wide for the reptiles in these hibernacula; in a group of garter snakes hibernating in the same ant hill, for instance, emergence extended over more than two months.

In most species the breeding season seems to be correlated with emergence from hibernation. In the five-lined skink for example, warming after a brief period of partial dormacy was found to initiate the breeding cycle, causing development of breeding colors in the male followed by courtship and copulation (Fitch, 1954:46). In some of the snakes, the advent of cool weather in autumn seems to inaugurate the sexual cycle, which is perhaps merely interrupted by the period of dormancy. Ring-necked snakes have been found copulating in October. On many occasions the males of the pilot black snakes, blue-racers, and copperheads removed from traps in cool weather of late October or early November everted their hemipenes and appeared to be in breeding condition.

TABLE 5.—BODY TEMPERATURES AND LENGTH OF SEASON OF ACTIVITY IN THOSE SPECIES OF AMPHIBIANS AND REPTILES FOR WHICH MANY RECORDS ARE AVAILABLE. PROBABLE OPTIMA AND PREFERRED RANGES ARE INDICATED TO NEAREST DEGREES. PREFERRED RANGE IS THAT IN WHICH RECORDS ARE CLUSTERED, BUT IN SOME INSTANCES THESE CONCENTRATIONS MAY REFLECT SPECIAL CIRCUMSTANCES OF COLLECTION RATHER THAN ACTUAL PREFERENCE.

	Body temperature				Average length of season of activity
	Number of records	Probable optimum	Preferred range	Observed range	
Bufo americanus	68	28	31–26	32.3–17.5	April 18 to late October (?)
Acris gryllus	74	29	32–20	34.8– 8.3	Year-round except in freezing weather
Pseudacris nigrita	16	28	31–27	30.3– 4.1	Year-round except in freezing weather
Hyla versicolor	48	28	31–26	33.7–19.7	April 19 to late October
Gastrophryne olivacea	104*	28	33–24	35.7–15.5	April 18 to October 17
Rana pipiens	50	28	31–24	33.6–21.4	Almost yr.-round except in freezing weather
Terrapene ornata	55	28	30–24	35.9–13.0	May 7 to October 14
Crotaphytus collaris	425	38	41–35	43.3–20.7	April 26 to October 7
Ophisaurus attenuatus	29	32	34–26	34.7–17.7	May 8 to October 10
Cnemidophorus sexlineatus	45	40	41–35	41.5–34.6	April 26 to October 3
Lygosoma laterale	16	29	31–27	33.5–22.0	Late March to late October
Eumeces fasciatus	56**	33	35–27	37.0–16.0	March 26 to early November
Eumeces obsoletus	17**	34	36–32	36.3–23.3	April 13 to October
Tropidoclonion lineatum	11*	31	32–29	32.4–25.5	Mid-April to ?
Diadophis punctatus	145*	28	31–21	32.3–11.7	March 25 to October 23
Carphophis amoenus	20*	27	30–24	31.7– 3.5	Late March to late October
Coluber constrictor	29	31	36–25	37.4–20.0	April 17 to November 7
Elaphe obsoleta	53	28	31–24	38.0–18.2	April 15 to October 25
Agkistrodon contortrix	59	27	30–25	34.5–17.5	April 19 to November 10

* Mostly found under rocks.
** Found in the open; many others were found beneath rocks.

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26-1202

(Continued from inside of front cover)

14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15, 1951.
15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.
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18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
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23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
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28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
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34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
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Index. Pp. 647-676.

***Vol. 6.** (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.

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(Continued on back of cover)

(Continued from inside of back cover)

4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
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7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
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Index. Pp. 625-651.

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Food of the Crow, Corvus brachyrhynchos Brehm, in South-central Kansas

BY

DWIGHT PLATT

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FOOD OF THE CROW, CORVUS BRACHYRHYNCHOS BREHM, IN SOUTH-CENTRAL KANSAS

By

Dwight Platt

Introduction

The yearly diet of the crow was studied from December, 1952, to February, 1954, in Harvey County and the northeastern townships of Reno County, in south-central Kansas. In the United States much attention has been devoted previously to the food taken by the crow because it is of economic importance. The work of Barrows and Schwarz (1895) was the first of a series of studies made by the United States Department of Agriculture. Kalmbach (1918, 1920, 1939) continued these studies by analyzing stomach contents from various parts of the United States. Also the diet of the crow has been studied by local areas (Imler—Oklahoma, 1939; Hering—New York, 1934; Black—Illionis, 1941; Lemaire—Louisiana, 1950).

I am grateful to Dr. Henry S. Fitch, for many valuable suggestions and helpful encouragement given in the course of my study. Professor E. Raymond Hall, who read the manuscript, likewise offered valuable suggestions. Dr. R. L. McGregor and Mr. Wilford Hanson provided invaluable assistance in identification of plants and insects found in the crow pellets.

Methods

Previous studies were based mostly on analyses of stomach contents. My study is based on the analysis of 617 regurgitated pellets collected from roosts and lookout posts. Fifty-three collections of pellets were made throughout the year at regular intervals, except that none was made in January, March, or May. The pellets were wrapped individually in paper or leaves as collected, and each was analyzed separately. The percentages by bulk of different food residues (excluding sand and other extraneous material) were estimated in each pellet and recorded.

Description of the Study Area

The study area is on the eastern edge of the Great Bend Prairie physiographic province of Moore (1930). The climate is characterized by moderate precipitation (ann. 30″), a wide range of temperature variations, moderately high wind velocities, and comparatively rapid evaporation. The summers are generally hot, and the winters are moderately cold but are free from excessive snowfall. The weather during the study period was unusually dry, and the summer temperatures were above normal. A drought had begun in 1952, following the cool and wet summer of 1951.

The study area includes the zone of transition from bluestem or tall-grass prairie to the buffalo grass or short-grass prairie. The principal farm crop in the study area is wheat. Sorghum grain, oats, hay crops (especially alfalfa), and corn are also grown. The study area supported a small population of breeding crows; an estimate based on field observations mainly in eastern Harvey County, was not more than one pair per square mile. In winter a large population of crows migrates into the area from the northern Great Plains. Censuses showed that on parts of the area the feeding population might be as great as 180 birds per square mile. These wintering crows concentrate in the western part of the study area where the flat, fertile wheat fields of central Harvey County are replaced by sand dunes and the sandy Arkansas River Valley. Here much land is devoted to raising livestock, and sorghum grain is an important field crop. There is also more waste land there than elsewhere in the area.

Data From Analysis of Pellets

Data obtained from the analysis of pellets were grouped in biweekly collections, and percentages of various food residues in the pellets collected within each biweekly period were averaged. Also frequency of occurrence was computed, and maximum and minimum percentages were included to permit a broader interpretation. In determining the minimum percentage, only those pellets were considered in which the food residue was present.

Pellets from roosts of resident crows were collected on a year round basis in eastern Harvey County near Newton (see tables 1 and 2). The data from these pellets were interpreted separately from data on collections made in the western part of the study area from under roosts of wintering crows (see tables 3 and 4).

In studies of the food of owls analysis of materials in regurgitated pellets has been widely used, but with crows this method has been little used because the nature of their food makes identification of material more difficult. Analysis of pellets has certain merits, however, and, if closely correlated with field studies, can give valuable information concerning food habits. The availability of pellets and the ease of collecting them are obvious advantages. Under large roosts in winter the number that can be collected is almost unlimited. At other seasons, pellets are scarcer, but even so they usually are more available than stomachs.

The technique of pellet analysis is more easily applied to a study of the yearly diet than is the technique of stomach analysis. The crow is euryphagous and, as shown by this study, the diets of crows a few miles apart may differ. Therefore a study made on a limited area within one biotic community, on a year round basis, and correlated with changes in the habitat should be of greatest value. For such a study, collection of stomachs is not practical unless individuals are abundant so that many can be sacrificed, but collection of pellets is practical and profitable.

One limitation of data based on material from pellets is the impossibility of closely correlating the volume of indigestible residues with the proportion of food items actually eaten. Such correlation is prevented not only by the different percentages of indigestible residues in different food items but also by irregularities in regurgitation and in the efficiency of the crow's digestive system. Barrows and Schwarz (1895:24-25) cite several instances of such irregularities in captive crows. In certain pellets that I studied, part of the wheat or other grain was undigested or partly digested, whereas in other pellets the only residue was finely divided chaff. Certain foods that lack hard parts may leave no recognizable residues in pellets. A captive crow that I raised did not form pellets when fed soft food. Nevertheless, data from analysis of pellets when supplemented by field observations, should serve as a sound basis for valid conclusions concerning the relative proportions of various foods eaten. The following field observations of habitat factors aid in interpreting the information obtained from pellet analysis.

Field Observations and Correlations

RESIDENT CROWS IN EASTERN HARVEY COUNTY.—Although no field observations were made on feeding behavior in April, the large percentage of oat hulls found in the pellets suggests that newly sown fields of oats must have been one of the major feeding grounds in that month. Oats were planted between February 15 and March 20.

The pellets collected in June were all from the roost of one family group of crows. This group spent much time in a cherry orchard and in the shelterbelt near it. Residues of cherry and wheat constituted the only plant foods found in the pellets. In both frequency and percentage, scarabaeid beetles constituted the other important food source. The wheat harvest started on June 17.

The cherry harvest was over by June 29. Grain harvest was over and the fields were being plowed by July 2. Alfalfa was being cut for hay in early July and crows were then feeding on plowed fields and the newly mown alfalfa fields. Much time in the middle of the day was spent along the creeks where crayfish could be obtained. During most of the summer, pellets were difficult to find because the roosts were small, shifting, and scattered and because few pellets were produced. For weeks at a time there were no usable pellets under roosts occupied by hundreds of birds, although droppings and feathers were present. At other times large collections of pellets could be gathered from small roosts. Plowing was a major farm operation at the season when pellets were most scarce. Larvae of insects (especially beetles), and earthworms might have provided a major source of food which lacked sufficient indigestible material to form pellets. A few feces were collected and analyzed in an attempt to find the residue of such soft-bodied foods. Indigestible materials were found in the feces, but these were of the same types as those found in the pellets. Only a few fragments were found which might have been the mouthparts of grubs.

After mid-July pellets were common under one small roost. In late July they were scarce, even at a roost with several hundred crows. The principal feeding grounds of crows were stubble fields and plowed fields. All grain picked up at this time was waste. Plowing was interrupted by rain from July 11-18 but was the major farm operation again after July 19.

From late July into early September crows fed in plowed fields, stubble fields, pastures, and newly mown hay fields. Pellets were scarce, considering that hundreds of crows used the roost where pellets were collected. Plowing was almost over by July 31. Brome grass was in full head during the early part of this period. Corn was in the milk stage during the early part of August but did not show up in any pellets. Although Sudan grass was in head during the early part of this period, other sorghum did not head out until September.

From early September to early October sorghum was in full head. The crows spent most of their feeding time in plowed fields, stubble fields, or pastures. Much time was spent along creeks where pools, which contained many small fish, were drying. Pellets were common under a small roost. Grasshoppers and beetles were the two staple foods in the diet at this time, as shown by their high frequencies and high percentages in pellets. The high percentage and frequency of wheat corroborates the observation that most of the feeding was being done in wheat fields. The relatively large percentages of fish bones, crayfish, and snail shells can be correlated with the observation that much time was spent by the crows at the pools in creek beds. Many ants were in the pellets. The total percentage of animal materials in the pellets was much higher in this period than in other periods. Plant material had been the highest, percentagewise, during most of the summer, except in the latter part of July. Most studies of food of the crow have shown a higher content of animal material during the summer than does my study. It would seem that much of the food material which did not show up in pellets during the summer was animal material.

Grasshoppers predominated in the diet in early October; some pellets consisted of little other than grasshopper mandibles and leg joints. Wheat is sown in this area from September 10 to October 15, most of it being sown after October 5, the recommended Hessian fly-free date. Most of the grain sorghum is harvested by mid-October. However, the utilization of both of these items was low in October. By October 10 only one pool was left in the creek bed under observation. The amount of fish bones, crayfish, and snail shells in the pellets decreased during this period.

Killing frosts occurred in mid-October. The percentage of grasshoppers in the diet then declined rapidly and later in the autumn declined more slowly. Nevertheless, grasshoppers and beetles remained the predominant animal-food residues into December and frequencies of occurrence remained relatively high.

As autumn progressed and insects became scarcer, plant material made up an ever-larger percentage of the diet. Wheat and sorghum constituted more than one-half of the food residues in this period. However, in December utilization of sorghum by resident crows in eastern Harvey County decreased. Sorghum is not an important crop in this area.

ROOSTS OF WINTERING CROWS.—The collections of pellets from roosts of wintering crows in western Harvey County and northeastern Reno County differed in having a higher percentage of plant material. Sorghum, corn, and wheat predominated in early autumn, while sorghum, sunflower seed, and corn predominated in the winter. Ants were utilized to a much greater extent in early autumn. For grasshoppers and beetles, frequency of occurrence was high but percentages were low. Most of the standing water in the sand dune country had dried approximately one year before, and the aquatic component of the diet was almost entirely lacking.

The two principal food items taken by crows in the winter of 1953 were grain sorghum and sunflower seed. Censuses in late November and late December, 1953, showed that feeding was mostly in harvested sorghum fields and corn fields, but alfalfa fields, wheat fields, plowed fields, and native pasture were also utilized.

Sorghum and sunflower seeds were also the staple foods during December, 1952. Oats and wheat showed higher percentages than in 1953, perhaps because different foods were available in these two winters or because of differences in locality. The pellets collected in 1952 were from western Harvey County, whereas most of those collected in 1953 were from northeastern Reno County.

The collection taken in February, 1954, showed a large percentage of oats in the diet. Newly sown oat fields were probably a major source of food at that time.

Economic and Ecologic Significance

The chief factors that determine the economic bearing of crows locally are: the yearly diet, the time of year in which each food item is taken, and fluctuation in the population density at different times of year. In the study here reported upon, the yearly diet was computed by averaging the percentages of each item determined for each biweekly period. Of the twenty-one collecting periods shown in the tables, six are overlapping pairs; that is to say, each includes one collection from eastern Harvey County and one from the western part of the study area. The average of these pairs was used in computing the yearly average. The yearly average is therefore based upon eighteen separate samples.

The percentages are weighted toward the food items taken in summer and autumn, since many biweekly periods in late winter and early spring are not represented. Of the collecting periods represented, two were in spring, six were in summer, seven were in autumn, and three were in winter. Pellets collected at a number of different localities are averaged together as a percentage; consequently the figures obtainable do not necessarily represent the diet of any one group of crows. Nevertheless the percentages obtained by this method are perhaps valid as a general indication of the diet of the crows in this area.

In my samples, plant material amounted to 69 per cent of the indigestible residues. Similar percentages have been found in other studies, ranging from 57 per cent (Barrows and Schwarz, 1895:72) to 71.86 per cent (Kalmbach, 1918:43). The percentage of plant material was highest in the winter. In one collection from a wintering crow roost it amounted to 99.5 per cent. In December in eastern Harvey County it averaged only 85.3 per cent. The lowest percentage (20) was found in the first half of October in eastern Harvey County when grasshoppers amounted to more than half the diet. At this same time pellets collected from the wintering roosts contained 72.4 per cent plant material.

Percentages of the chief items in the total food residues, and (in parentheses) number of sampling periods in which each item was represented, are shown in the following list: wheat 23.2 per cent (20), sorghum 15.2 (16), oat 7.8 (8), sunflower 7.2 (8), corn 5.4 (12), brome 4.2 (5), other grass 2.4 (7), cherry 1.2 (2), beetle 13.3 (21), grasshopper 9.3 (19), ant .7 (3), miscellaneous insect .2 (2), mammal 2.6 (19), bird .8 (1), eggshell .5 (3), snake .1 (2), fish .9 (9), crayfish 2.4 (12), snail .2 (9).

Wheat is the "staff-of-life" of the crows in south-central Kansas and the percentage recorded in the diet in my study is much higher than the percentages found by other investigators. Wheat, being the principal crop in this area, was a readily available food. The fluctuations in the use of wheat were due to fluctuations in the availability of other foods that were preferred. In eastern Harvey

County wheat consumption was 35.7 per cent of the diet in the latter part of July, and 49.1 per cent in December.

Consumption of wheat was high (34.4 per cent) during the harvest in June. However, this does not indicate serious damage since the crow population at this time was low, and much of the wheat eaten probably was shattered waste grain. When plowing began, wheat consumption was much reduced. At the time wheat was sown, September 10 to October 15, consumption was average to low.

In western Harvey County wheat was less important in the diet of wintering crows. After reaching a peak (22.7 per cent) in October, just after sowing, it steadily decreased, varying from 6.9 per cent to none in December.

The wheat consumption of crows has little significance economically. No instances of damage were reported to me either at the time of harvest or at the time of sowing. Although crows undoubtedly do eat wheat from newly sown fields, this utilization seldom damages the stand. No evidence of pulling young wheat was found. Most wheat eaten was waste grain.

Grain sorghum was the staple food of the wintering crows. In eastern Harvey County, where sorghum is not an important crop, its consumption began in August, reached a peak in the last part of November, and fell off sharply in December. The grain sorghum crop is vulnerable to damage by crows and it is ripening in the autumn as the crow population is building up. In certain areas and certain years the loss may be important. An exceptional instance was reported to me of crows taking 40 per cent of the crop from a small field of early ripening sorghum near a roost. Most farmers and county agents interviewed thought that the over-all damage was not great. The crop is usually combined and little remains in the fields after October, when the majority of wintering crows arrive. Nevertheless, even waste grain picked up after harvest should be counted as a loss on some farms where stock are turned in to clean up such grain.

Oats were taken sparingly as waste grain in summer, autumn, and winter, and most were eaten in late winter and early spring from newly sown fields (37.2 per cent of the February diet and 72.6 per cent of the April diet). These percentages were probably high, since there is a high proportion of indigestible residues in oats. This is more than compensated for in the yearly average by the paucity of collections made in the period when consumption of oats was highest.

Fields newly sown to oats provided a major supply of food in the early spring when other food supplies had been depleted. However, no instance of damage to a stand of oats was reported to me. Aldous (1944:294) mentioned that crows fed on spring-sown oat fields in Oklahoma but suggested that they picked up only grain which was not covered.

Sunflower seeds, although not important as a food of the crows in eastern Harvey County, were a staple food of these wintering in the western part of the study area. Consumption of sunflower seeds began in September. In the latter part of December the percentage increased and many pellets were composed entirely of sunflower seed hulls. Sunflower seeds have a high percentage of indigestible residue.

In both popular accounts and scientific studies, the economic significance of the consumption of weed seeds such as those of sunflowers by birds often has been interpreted in an oversimplified manner. It has been assumed that if crows eat several million sunflower seeds in the winter, the sunflowers growing in the farmers' fields the next year will have been reduced by the same number. However, like most annual plants, sunflowers produce a great surplus of seeds each year. Most of the seeds consumed by crows would never have a chance to grow to maturity, even if they were not eaten. Therefore this component of the crow's diet is only slightly beneficial or neutral for the farmer. The effect of crows (or of the entire bird population for that matter) upon the sunflower crop in the farmers' fields is probably slight.

Corn is one of the preferred foods of crows, but little corn was grown in the study area. Other investigators have found higher percentages elsewhere. In eastern Harvey County corn reached its highest point in December but was insignificant in the diet. In the western part of the study area it made up a larger percentage of the diet of wintering crows. The corn eaten early in the season was undoubtedly from the standing crop. However, most of that picked up in late autumn and in winter was waste grain. Since little corn was shocked and left in the fields, there was less opportunity for damage. The amount of corn pulling at planting time was not determined, since no pellets were collected then. However, the population of crows at that time was low. I received no complaints of such damage to corn nor of significant damage to the corn crop at other seasons.

There were pastures of brome grass in the area under study in eastern Harvey County, and the seeds seemed to be a preferred food, constituting a major food supply for the crows in the latter part of July and the first part of August. Having a high content of indigestible residues they probably showed up in the pellets in percentages out of proportion to their importance in the diet. They were unimportant in the diet of wintering crows in the western part of the study area. This component of brome grass in the diet was economically of little significance in the study area, although it could be of significance where brome grass seed was being harvested.

Cherries were recorded only in June and only from one family of crows in eastern Harvey County; cherry orchards are few in this area. The damage done by the crows in the cherry orchard was slight, since only a few crows fed there.

Weed seeds such as those of spurges (*Euphorbia*), ragweed, and pigweed were found in trace amounts in the diet of the crows. However, they were not preferred foods, since they were available in large quantities.

Wild fruits such as grape and pokeberry also showed up in trace amounts. Elsewhere, investigators have found wild fruit forming a major source of food in winter. However, it was not readily available in this area.

Plant fibers and seeds unidentifiable with the resources at hand formed 2.2 per cent of the residues.

It was reported to me that crows caused damage to watermelons which are extensively grown in the sandhills region but no residues of this crop were found in any pellets collected.

Insects were most important in the animal portion of the food. The economic and ecologic significance of insects in the diet of birds is often oversimplified. The effects of predation upon animal populations are complex, and predation is often a by-product of population rather than a controlling factor.

A female insect eaten before oviposition has a greater ecologic significance than one eaten after she has laid her eggs and is ready to die.

Beetles made up more than half of the insect component of the diet. Scarabaeids were readily recognizable. Other beetles were classified as predaceous or non-predaceous according to the type of mandibles found. When mandibles were lacking the occurrences were listed merely as unclassified beetles, and those made up 5.6 per cent of the yearly food residues. Predaceous beetles made up 3.3 per cent, whereas non-predaceous beetles made up only 1.3 per cent. Both were found in one-half of the collecting periods. Predaceous and non-predaceous beetles formed 1.2 per cent of the yearly food residues. This preponderance of predaceous beetle material is what might be expected from the manner in which crows feed. Many predaceous ground beetles of the family Carabidae would be found under rocks and clods and on the ground.

Beetles were a constant component of the diet in summer. They reached a peak of 48.7 per cent in the last part of July. In November the percentage declined and by December they formed only 2.5 per cent of the diet.

Scarabaeid beetles were utilized in large quantities when they were most abundant; they made up 28.7 per cent of the diet in the latter part of June. The larvae of scarabaeid beetles are destructive to wheat and alfalfa and live in the ground from one to three years before metamorphosing into adult beetles. Adults emerge from the ground from April to mid-August, the maximum flight occurring in May and June. Most of the eggs are laid from the last of May to the middle of July (Hayes, 1920:306). Afterward the adults soon die. Many of the beetles are nocturnal, but some of the more important destructive forms are diurnal (Hayes, 1918: 142). Crows pick up the diurnal forms when they are active and perhaps find the nocturnal forms under clods or in burrows and eat them in ecologically significant numbers.

Crows are beneficial to the farmer insofar as they control the populations of scarabaeids and other non-predaceous beetles. However, destruction of predaceous beetles is harmful to the farmers' best interests.

Grasshoppers, second only to beetles in the insect component of the diet, are among the most destructive insects in Kansas. Eggs laid in autumn overwinter and hatch the next summer, from April to August, depending upon the species. The maximum numbers of grasshoppers are present in late summer and early autumn and they continue feeding on crops until the first killing frost. The greatest damage is caused by the destruction of the foliage of corn, wheat, and alfalfa (Smith, *et al.*, 1943:126). The consumption of grasshoppers closely followed the curve of their availability, since they are a preferred food of the crow. They were picked up in small quantities even in winter. In summer they made up 6 to 10 per cent of the diet of the crows in eastern Harvey County. Through the late summer and autumn this percentage rose, until during the first half of October they made up 59.6 per cent of the diet. However, in the western part of the study area, they constituted a smaller part of the diet.

Predation upon grasshoppers, especially in summer and early autumn, benefits the farmer by helping to stabilize populations of grasshoppers. However, when grasshopper consumption was highest, in early October, many of those eaten probably already had completed their breeding cycle, and their consumption was hence of little significance economically or ecologically.

Ants were consumed only in September and October when they constituted as much as 14.9 per cent of the diet. Crows may make an entire meal from a large colony; at any rate, whenever ants were found in a pellet, they constituted a large percentage of it.

Miscellaneous insect remains constituted two-tenths of one per cent of the yearly diet. Hemipteran remains were present only in trace quantities (.5 per cent of the July 13-26 sample from eastern Harvey County).

Only a few questionable fragments from insect larvae were found in the pellets collected in the course of this study. However, as mentioned earlier, there is evidence that larvae constituted a major food supply during much of the summer.

Many investigators have found that crows feed on grubs and caterpillars (Aldous, 1944; Alexander, 1930; Lemaire, 1950; Kalmbach, 1918; Barrows and Schwarz, 1895). A number of county agents with whom I had correspondence mentioned that crows aided the farmer in this way. More investigation is required to determine the significance of crow predation upon insect larvae in this area. Most of the bone material recorded was fragmentary. Phalangeal or podial elements of rodents and various bones of rabbits were identified. The only teeth identified were those of the genus *Rattus*. Barrows and Schwarz (1895:24-25) found that small bones of mammals may be completely ground up and digested by the crow. Hence the amount of food furnished by mammals, either alive or as carrion, may be higher than my figures indicate.

Bones of birds were found in only one pellet, obtained in early July. However, few pellets were collected in the nesting season.

The eggshell occurring in the pellets probably was indicative of extensive feeding on dumping grounds, and I received no reports of eggs lost to crows on poultry farms. Such damage has been reduced to a minimum since most poultry flocks are well-housed.

The percentage of aquatic animals (fish, crayfish and snail) in the diet increased during the early autumn, as the creeks dried up in eastern Harvey County, but after mid-October declined rapidly, as all the pools were then gone.

Conclusions

The large wintering flocks of crows are important consumers of grain sorghums in south-central Kansas. In the early autumn when the crow population is building up, it damages the sorghum crop before harvest. The damage varies from year to year, being much more keenly felt in dry years when the crop is poor or in years when the crop is late. However, most of the sorghums, which are the principal item of diet of these wintering crows, are waste grain taken from the fields after harvest. Some of this waste grain taken should be counted as a loss because the farmer would normally let his livestock utilize it.

Crows use newly sown oat fields as a major source of food during the late winter and early spring. However, damage to the crop is slight. Corn is not an important crop in this area. The crow population is low at the season when corn is planted, so probably little damage is done at this time. Much of the corn eaten in winter is waste grain. Feeding on wheat is of little economic importance, since most of that taken is waste grain. Feeding on sunflower seeds may be counted as neutral to slightly beneficial. Damage to watermelons, which are extensively grown in the sandhills region, may be important at times. Crow feeding upon other crops is only locally significant.

Although it has food preferences, the crow is euryphagous, and its diet is governed to a large extent by the availability of various types of food in its habitat. Therefore, in its ecologic relationships with many other species, it is a density dependent predator. It reduces the numbers of a certain species when the latter becomes unusually abundant but lessens the mortality pressure against it when the prey population is low. Predators of this type tend to maintain stability in a community in contrast to the violent oscillations often caused by a more stenophagous predator. This study indicates that in south-central Kansas crows help to stabilize the populations of grasshoppers, ground-dwelling beetles both predaceous and non-predaceous, and probably those of other types of insects whose soil dwelling larvae are subject to predation during summer plowing.

Crows also serve as scavengers, feeding on carrion and at dumping grounds, as indicated by the high frequency of eggshell and mammalian bone in the diet. Bird bones were found in an insignificant amount in this study, but extensive collections were not made during the main nesting season.

Summary

An intensive study of the yearly diet of crows was carried on from December, 1952, to February, 1954, in Harvey County and the northeastern townships of Reno County, Kansas, in order to discover some of the ecologic and economic relationships of the population of crows in south-central Kansas. The study is based upon the analysis of 617 regurgitated pellets collected throughout the year. Data obtained from this analysis have been correlated with field observations on crows and habitat changes.

The area is in the zone of transition between tall-grass and short-grass prairie, and the predominant agricultural crop is wheat. The study area supports a breeding population of approximately one pair of crows per square mile, but large flocks of wintering crows move into the western part of the area near the Arkansas River Valley.

Plant material amounted to 69.0 per cent of the pellet residues. Wheat is the food taken in greatest amount in the yearly average, but the staple foods of the wintering crows are grain sorghum, sunflower seeds, and corn. Crows use newly sown oat fields as a major source of food in late winter and early spring, but damage to the crop seems to be slight. Growers of grain sorghum and, locally, growers of corn and watermelons, sustain serious damage from crows.

Being euryphagous, crows exert a stabilizing influence on many kinds of prey and on the biotic community as a whole. This study indicates that their effects are especially important in helping to stabilize the populations of grasshoppers and of ground-dwelling beetles, and possibly those of some other insects that have soil-dwelling larvae.

Carrion and material from dumping grounds furnish another fairly constant component of the crow's diet.

TABLE 1. AVERAGE, MAXIMUM, AND MINIMUM PERCENTAGES OF FOOD RESIDUES IN PELLETS COLLECTED IN EASTERN HARVEY COUNTY, IN 1953.

	April 6–19	June 15–28	June 29–July 12	July 13–26	July 27–Aug. 9	Aug. 10–23	Sept. 7–20	Sept. 21–Oct. 4	Oct. 5–18	Oct. 19–Nov. 1	Nov. 2–15	Nov. 16–29	Nov. 30–Dec. 13
Number of pellets	9	7	6	19	18	5	57	29	27	24	25	7	8
No. of collections	1	4	4	4	4	2	5	4	4	3	5	1	2
wheat	18.2 (90–5)	34.4 (99–50)	1.7 (10)	35.7 (80–10)	28.5 (80–5)	29.0 (55–20)	23.4 (100–5)	21.5 (100–5)	10.8 (60–15)	35.4 (85–10)	33.0 (80–35)	43.7 (98–30)	49.1 (98–20)
sorghum	......	......	......	......	2.0 (35)	......	10.7 (90–10)	14.0 (75–5)	7.6 (60–3)	24.4 (85–5)	24.7 (100–10)	28.6 (80–5)	6.9 (40–15)
oats	72.6 (99–50)	......	......	1.6 (30)	......	......	......	......	......	......	......	......	......
sunflower seed	......	......	......	......	......	......	......	......	......	......	......	6.4 (40–5)	......
corn	......	......	......	......	......	......	......	......	......	4.5 (50–10)	4.0 (80–10)	1.4 (10)	15.0 (70–50)
grass seed	......	......	......	.5 (5)	44.6 (90–60)	28.6 (85–5)	4.8 (70–5)	......	......	......	......	......	......
grape	......	......	......	......	......	......	.1 (2)	......	......	......	......	......	......
cherry	......	20.1 (70–20)	1.7 (10)	......	......	......	......	......	......	......	......	......	......
spurge	......	......	.8 (5)	.1 (2)	......	......	......	......	......	.2 (5)	......	......	......
misc. plant	......	......	......	1.6 (30–10)	5.2 (95)	......	......	4.4 (90–40)	1.6 (45)	2.1 (50)	5.5 (75–10)	2.9 (20)	14.3 (70–45)
TOTAL PLANT	90.8	54.5	4.2	39.5	80.3	57.6	39.0	39.9	20.0	66.6	67.2	83.0	85.3

scarabaeid beetle	....	28.7 (75–25)	5.0 (30)	....	....	....	....	....	....	....	....	....	....
other beetle	2.7 (10–5)	.1 (3)	34.2 (100–20)	48.7 (90–10)	10.0 (90–10)	21.0 (45–10)	19.0 (80–5)	10.6 (95–5)	15.5 (98–1)	13.9 (70–5)	14.4 (65–5)	5.3 (15–2)	2.5 (20)
grasshopper	....	.1 (2)	6.6 (40)	10.9 (40–5)	4.2 (40–5)	15.0 (30–5)	23.4 (100–5)	36.3 (95–5)	59.6 (90–34)	11.8 (65–5)	14.3 (99–5)	10.3 (65–2)	4.4 (10–5)
ant	....	....	....	....	....	....	5.9 (90–75)	....	....	....	....	....	....
misc. insect	....	....	....	.5	....	....	1.9 (50–5)	2.8 (60)	....	....	....	....	....
crayfish	.5 (5)	1.5 (10)	35.0 (100–10)	....	.6 (10)	1.0 (5)	1.2 (25–10)	.2 (5–2)	.4 (5–2)	1.4 (20–10)	....	....	....
snail	....	....	....	....	.6 (10)	....	.6 (10–2)	1.3 (20–5)	trace (1)	1.1 (10–5)	.2 (5)	....	....
fish	....	....	....	.1 (7)	....	.1 (5)	4.8 (20–5)	7.3 (20.5)	2.5 (20.1)	3.4 (20–5)	.6 (10–5)	....	....
bird	....	....	15 (90)	....	....	....	....	....	....	....	....	....	....
eggshell	....	....	....	.3 (5)	.6 (10)	3.0 (10–5)	2.0 (30–5)	1.1 (10–5)	.4 (1)	.2 (5)	.8 (20)	.7 (5)	....
mammal	6 (45–10)	15.1 (100–5)	....	....	3.7 (50–5)	1.4 (5–2)	2.2 (60–2)	.5 (5)	1.6 (20–2)	1.6 (10–5)	2.5 (20–1)	.7 (5)	7.8 (25–2)
TOTAL ANIMAL	9.2	45.5	95.8	60.5	19.7	42.4	61.0	60.1	80.0	33.4	32.8	17.0	14.7

TABLE 2. FREQUENCIES OF OCCURRENCE OF FOOD RESIDUES IN PELLETS COLLECTED IN THE EASTERN PART OF HARVEY COUNTY—1953.

	April 6–19	June 15–28	June 29–July 12	July 13–26	July 27–Aug. 9	Aug. 10–23	Sept. 7–20	Sept. 21–Oct. 4	Oct. 5–18	Oct. 19–Nov. 1	Nov. 2–15	Nov. 16–29	Nov. 30–Dec. 13
No. of pellets	9	7	6	19	18	5	57	29	27	24	25	7	8
wheat	6	3	1	18	16	4	27	12	10	15	13	4	6
sorghum	....	....	....	....	1	....	20	12	10	12	12	4	2
sunflower seed	....	....	....	....	....	....	....	....	....	....	....	2	....
oats	8	....	....	1	....	....	....	....	....	....	....	....	....
brome grass	....	....	....	2	10	4	....	....	....	....	....	....	....
corn	....	....	....	....	....	....	....	....	....	3	3	1	2
cherry	....	3	1	....	....	....	....	....	....	....	....	....	....
grass seed	....	....	....	....	....	....	11	....	....	....	....	....	....
spurge	....	....	1	1	....	....	....	....	....	1	....	....	....
grape	....	....	....	....	....	....	1	....	....	....	....	....	....
misc. plant	....	....	....	2	1	....	....	2	1	1	3	1	2
beetle (scarabaeid)	....	4	1	....	....	....	....	....	....	....	....	....	....
beetle (other)	4	1	4	19	5	5	39	15	17	16	14	4	1
grasshopper	....	1	1	12	6	5	39	22	24	12	18	3	6
ant	....	....	....	....	....	....	4	....	....	....	....	....	....
bug (hemipteran)	....	....	....	1	....	....	....	....	....	....	....	....	....
misc. insect	....	....	....	....	....	....	3	1	....	....	....	....	....
crayfish	1	1	3	....	1	1	3	2	2	2	....	....	....
snail	....	....	....	....	1	....	7	4	1	4	1	....	....
fish	....	....	....	2	....	1	28	14	7	7	2	....	....
bird	....	....	1	....	....	....	....	....	....	....	....	....	....
eggshell	....	....	....	1	1	2	10	5	8	1	1	1	....
mammal	2	2	....	....	4	2	8	3	5	5	8	1	5

TABLE 3. AVERAGE, MAXIMUM, AND MINIMUM PERCENTAGES OF FOOD RESIDUES IN PELLETS COLLECTED AT WINTERING CROW ROOSTS IN THE WESTERN PART OF THE STUDY AREA—1952-53-54.

	Dec. 28–Jan. 11	Aug. 24–Sept. 6	Sept. 7–20	Oct. 5–18	Nov. 16–29	Dec. 14–27	Dec. 28–Jan. 10	Feb. 8–21
Number of pellets	62	5	38	65	56	22	96	32
No. of collections	1	1	1	1	3	1	1	1
wheat	6.9 (100–10)	62.8 (99–35)	14.6 (90–10)	22.7 (90–10)	2.2 (95–10)	....	3.3 (90–30)	2.8 (50–10)
sorghum	29 (100–5)	1 (5)	22.4 (95–5)	31.2 (100–10)	41.2 (100–5)	42.5 (100–5)	32.4 (100–10)	21.6 (100–10)
sunflower seed	26.3 (90–5)	....	3.3 (95–5)	5.0 (60–10)	26.9 (95–3)	22.0 (90–5)	32.4 (100–5)	21.6 (80–10)
corn	11.4 (100–10)	19.0 (40–15)	12.4 (95–5)	4.5 (85–30)	14.0 (100–5)	11.4 (100–10)	14.1 (100–5)	1.2 (20–10)
oats	14.1 (100–10)	....	....	4.9 (80–15)	5.7 (70–5)	5.5 (75–5)	4.6 (95–5)	37.2 (100–10)
brome grass	1.4 (85)	....	....	....	....	....	.1 (10)	....
other grass	9.4 (95–5)	....	....	3.2 (80–20)	4.0 (90–10)	15.7 (95–10)	8.8 (100–10)	6.3 (50–20)
grape	....	....	trace (2)	....	....	....	.1 (10)	....
pokeberry	....	....	.4 (15)	.5 (30–2)	....	....	....	....
spurge	....	....	....	.4 (25)	....	....	.2 (10–1)	....
ragweed	....	....	....	....	.1 (5)	....	.5 (10–5)	.2 (5)
misc. plant	1 (50–1)	....	.8 (30)	....	....	....	.8 (80–2)	.2 (3–2)
TOTAL PLANT	99.5	82.8	53.9	72.4	94.1	97.1	97.4	97.4
grasshopper	.1 (5)	6.0 (30)	8.9 (30–5)	10.5 (70–5)	1.4 (15–5)	....	.5 (15–5)	.3 (5)
beetle	.1 (5)	9 (15–10)	17.8 (95–2)	12.1 (80–3)	1.7 (15–2)	.9 (10–5)	.4 (10–5)	.9 (10–5)
ant	....	....	14.9 (95–73)	3.4 (85–5)	....	....	....	....
crayfish	....	....	.7 (10–5)	.8 (50)	....	....	.5 (50)	....
snail	.1 (5)	....	....	....	.1 (5)	....	.1 (5)	....
fish	....	....	.1 (5)	....	....	....	.1 (5)	....
snake	....	....	1.8 (60–5)	....	....	.9 (20)	....	....
eggshell	....	....	....	....	.3 (10–5)	.4 (10)	.6 (10–5)	1.1 (20–5)
mammal	.2 (10–5)	2.2 (5–1)	1.9 (20–5)	.8 (10–5)	2.4 (60–5)	.7 (10–5)	.4 (10–5)	.3 (10)
TOTAL ANIMAL	.5	17.2	46.1	27.6	5.9	2.9	2.6	2.6

TABLE 4. FREQUENCIES OF OCCURRENCE OF FOOD RESIDUES IN PELLETS COLLECTED AT WINTERING CROW ROOSTS IN THE WESTERN PART OF THE STUDY AREA—1952-53-54.

	Dec. 28–Jan. 11	Aug. 24–Sept. 6	Sept. 7–20	Oct. 5–18	Nov. 16–29	Dec. 14–27	Dec. 28–Jan. 10	Feb. 8–21
Number of pellets	62	5	38	65	56	22	96	32
wheat	11	5	10	27	3	......	5	4
sorghum	45	1	22	36	44	16	74	18
sunflower seed	43	......	5	12	32	9	68	19
corn	14	4	11	5	12	8	27	3
oats	18	......	......	8	9	3	12	24
brome grass	1	......	......	......	......	......	1	......
other grass	15	......	......	5	5	7	15	5
grape	......	......	1	......	......	......	1	......
pokeberry	......	......	1	2	......	......	......	......
spurge	......	......	......	1	......	......	5	......
ragweed	......	......	......	......	1	......	8	1
misc. plant	4	......	1	......	......	......	2	2
grasshopper	1	1	23	38	10	......	5	2
beetle	1	4	38	48	15	3	6	4
ant	......	......	7	6	......	......	......	......
crayfish	......	......	3	1	......	......	1	......
snail	1	......	......	......	1	......	1	......
fish	......	......	1	......	......	......	1	......
snake	......	......	2	......	......	1	......	......
eggshell	......	......	......	......	2	1	9	3
mammal	2	3	5	7	10	2	5	1

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ECOLOGICAL OBSERVATIONS ON THE WOODRAT, NEOTOMA FLORIDANA

By

Henry S. Fitch and Dennis G. Rainey

Introduction

The eastern woodrat exerts important effects on its community associates by its use of the vegetation for food, by providing shelter in its stick houses for many other small animals, and by providing a food supply for certain flesh-eaters. In the course of our observations on this rodent on the University of Kansas Natural History Reservation, extending over an eight-year period, from February, 1948, to February, 1956, these effects have changed greatly as the population of woodrats has constantly changed in density, and in extent of the area occupied.

This report is concerned with the population of woodrats on the Reservation, the changes that the species has undergone, and the factors that have affected it. Our two sets of field data, used as a basis for this report, supplement each other and overlap little, either in time or space. Fitch's field work which covered approximately the western half of the Reservation, was begun in September, 1948, and was pursued most intensively in the autumn of 1948 and in 1949, with relatively small amounts of data obtained in 1950 and 1951 because of the great reduction in numbers of rats. Rainey's field work began in the spring of 1951 and was continued through 1954, concentrating on a colony in the extreme northwestern corner of the Reservation and on adjacent privately owned land. In actual numbers of rats live-trapped and for total number of records the two sets of data are comparable. Fitch's field work consisted chiefly of live-trapping while Rainey's relied also upon various other approaches to the woodrat's ecology. Rainey's findings were incorporated originally in a more comprehensive report (1956), from which short passages have been extracted that are most pertinent to the present discussion. Our combined data represent 258 woodrats (153 Fitch's and 105 Rainey's) caught a total of 1110 times (660 Rainey's and 450 Fitch's). Rainey's records pertain, in part, to woodrats outside the Reservation but within a few hundred yards, at most, of its boundaries.

Habitat

In the autumn of 1948 the population of woodrats was far below the level it had attained in 1947 or earlier, but the rats were still abundant and distributed throughout a variety of habitats. Almost every part of the woodland was occupied by at least a sparse population. Also, many rats lived beyond the limits of the woodland proper, in such places as deserted buildings, thickets, roadside hedges, and tangles of exposed tree roots along cut banks of gullies. All these situations are characterized by providing abundant cover, a limiting factor for this woodrat.

In 1947, when the population of woodrats was especially high, plant succession on the wooded parts of the Reservation may have been near the optimum stage for the rats. For some 80 years, since the time the land was first settled and prairie fires were brought under control, woody vegetation has been encroaching into areas that were formerly grassland.

About 1934 the University changed its policy with regard to treatment of the tract that was later made the Reservation. Up to that time, most of the area had been used as pasture and subjected to heavy grazing, but several fields had been fenced and cultivated. Under the new policy the hillsides and hilltop edges with open stands of various deciduous trees were enclosed with stock fences and protected from grazing. Successional trends were greatly altered. Woody vegetation, already favored by protection from the prairie fires originally important in the ecology of this region underwent further development as a result of protection from browsing. Thickets of shrubs and saplings sprang up throughout the woodland, forming a dense understory layer beneath the discontinuous canopy of the relatively scattered mature trees. The composition and density of the undergrowth varied markedly in different parts of the woodland. The parts that were formerly most open acquired the most dense understory. Blackberry, honey locust, osage orange, and prickly ash formed in places thorny tangles almost impenetrable to humans. This thicket stage reached its peak in density in the middle to late forties coinciding approximately with the time of maximum abundance of the rats. In the past eight years, under continued protection from burning, cutting and browsing, the forest has developed further; sizable trees 20 feet or more high and up to eight inches in trunk diameter have grown from seedlings during the period of protection. An almost continuous canopy of foliage has developed, shading the understory and thinning it by killing shrubs and saplings. In those situations where the canopy is most dense, as on north slopes having stands of young hickory averaging twenty feet high, the understory is now largely lacking, but in other situations, particularly on south slopes, the understory thickets are still dense. On the whole, however, habitat conditions have become less favorable for the woodrat.

Within the woodland the population of woodrats was not evenly distributed even at its maximum density; only those situations that provided sufficient overhead shelter were occupied by woodrats. The hilltop limestone outcrop, which was the refugium of the survivors when the population was at low ebb, also supported the greatest concentration when the population was high. The number of individuals living along any particular stretch of ledge could be determined only by intensive live-trapping, whereas residences of individuals could be more readily identified in most other situations away from the ledge. Stick houses of woodrats are, characteristically, large and dome-shaped in woodland, but along the ledges they usually lacked this typical form and consisted of a much smaller accumulation of sticks, often merely filling a small crevice. Sticks carried into such places where they were partly or wholly protected from moisture and sunshine were much less subject to decay than those in more open situations, and remained long after the rats themselves were gone. Accumulations of droppings in depressions in rock surfaces beneath overhanging ledges likewise have lasted for many years. The rock outcrop provided a continuous travelway along the hilltops, and even parts that were not permanently occupied usually had some sign. The following types of situations were found to be especially favorable for occupancy: deep crevices beneath overhanging projections of the ledge; large flat boulders broken away from the main ledge; thick clumps of brush (usually fragrant sumac, *Rhus trilobata*) providing shelter and support for the house; logs fallen across the ledge providing support and protection for the house structure.

A second outcropping limestone stratum approximately 20 feet below the level of the hilltop was just as extensive as the upper outcrop, but it was little used by the rats because the exposed rock surface was more regular, lacking the jagged cracks and deep fissures of the hilltop outcrop; and it lacked the overhanging projections which provided overhead shelter for the rats along the upper outcrop. More than ninety per cent of the rats that were recorded as associated with the outcrops were at the hilltop stratum.

Second in preference to the hilltop outcrop as a house site was the base of an osage orange tree in thick woods. This tree occurs throughout the woodland of the Reservation, having become established when the leaf canopy was more open, and the whole area was subject to grazing, with less development of the understory vegetation in the woodland. Houses were most often situated in those osage orange trees that had been cut one or more times, and had regenerated with spreading growth form, the multiple branching stems offering substantial support. Occasionally houses were built in crotches from two to six feet above ground.

Blackberry thickets also are favorable locations for houses. These thickets grew up mostly in fenced areas from which livestock were excluded, but where there was not dense shade—hilltop edges and level or gently sloping ground adjacent to creek banks. The houses were usually in densest parts of the thickets where they were almost inaccessible. Mats of dead canes more or less horizontal, with the live canes growing up through them, provided effective overhead protection, while the ground beneath was relatively open. Houses built in the thickets were so well concealed that they were usually not detected until after leaves were shed in autumn. In most cases the blackberry thickets were small and well isolated. Houses of the rats were sometimes unusually near together suggesting that these thickets provided especially favorable habitat conditions.

Hollow trees are often utilized, the accumulation of sticks for the house being largely inside the cavity. To be suitable for a house site, the snag must have an opening near ground level, and another higher on the trunk, providing emergency outlets in two directions. Most of the hollow trees utilized were black oaks (*Quercus velutina*).

In 1948 there were many houses in cut tops of trees left from small scale lumbering operations a few years earlier. The densely branched tops of elms, oaks and hickories had satisfied the requirement for support of the house and nearby shelter. The houses built in them were in open woodland well separated from otherwise favorable situations. By 1948 the tops were disintegrating and no longer provided effective shelter. The houses built in them were falling into disrepair and were not permanently inhabited but were often used temporarily by wandering individuals.

Along cut banks of gullies where trees were partly undermined by erosion, the exposed, tangled root systems provided sites for occupancy. In these situations the accumulations of sticks were small and lacked the typical domed shape, consisting essentially of a lining to the cavity beneath the roots.

Two small buildings at the Reservation headquarters were accessible to woodrats and were utilized off and on throughout much of the period of this study, despite the fact that most other sites of occupation away from the hilltop outcrops were deserted in the same period. One small building used as a laboratory had an enclosed wooden box five feet square housing an electric water pump. The interior of this box was accessible to the rats from beneath the floor. Litter of sticks and stems and various food materials were carried in by the rats. The nest thus protected and enclosed was not surrounded by the usual accumulation of sticks. An old garage 30 feet from the laboratory building was also occupied, sometimes by a different individual. The nest and food stores were behind boards propped against the wall.

In October, 1948, live-trapping was begun on a heavily wooded slope facing northwest, and a ten-acre area was trapped rather thoroughly in the succeeding weeks. Because few traps were then available, this was the only area that was well sampled in 1948, although diffuse trapping was carried on over some 200 acres. On the ten-acre tract a total of 17 adult and subadult woodrats were caught, four along the hilltop rock outcrop, six along the gully at the bottom of the slope, and seven at intermediate levels on the slope. Judging from the many unoccupied houses, the population on this tract had been much higher before the study was begun. On the basis of this sample it seems that in 1947 a population of several hundred woodrats lived on the wooded parts of the square mile where the Reservation is located.

Reduction of Population

The abrupt reduction in the population of woodrats on the Reservation cannot be explained conclusively with available data. Probably weather played a major part, but other unknown factors must have been important also. It is certain that the population of woodrats was high, if not at an all-time peak, in 1947. In late February, 1948, when one of us (Fitch) first visited the area on a preliminary inspection trip (not concerned primarily with woodrats), houses of these rats were found to be unusually numerous and those seen seemed to be occupied and well repaired. Possibly the population was drastically reduced within the next few weeks, as unseasonably cold and stormy weather occurred in early March. For the first 12 days of March, 1948, temperature averaged 20° below that of average March weather, and even colder than the average for January or February. A reading of —5°F. on March 11 set a new low locally for the month since records were begun in 1869. The record low temperatures were accompanied by 12.8 inches of snow. This spell of unusually severe weather in early March coincided with the period in which first litters of young usually are born, as most females breed in early February and the gestation period is in the neighborhood of five weeks. That most of these first-litter young may have been eliminated by the unfavorable extreme of weather at the most critical stage in the life cycle may be readily imagined although definite proof is lacking. However, the mortality must have extended beyond newborn young. Loss of first litters ordinarily would be compensated for by the end of the season, since a female usually breeds more than once in the course of a season. In any case, by autumn, when the actual field study of woodrats was initiated, many houses were already deserted and in disrepair. Although the rats were still moderately abundant, they were, seemingly, much below the population peak of the preceding year.

Further drastic reduction of adults and subadults took place in the winter of 1948-49. In the course of live-trapping operations from mid-October into early December, 51 individuals were caught and marked. Chiefly because of unfavorable weather conditions, field work was discontinued in mid-December, and live-trapping was not resumed until early March. Subsequently, only 12 of the woodrats previously marked could be recaptured, and the population had become noticeably sparse. Seemingly, more than three-fourths of the population present in late autumn had been eliminated in the interval. In January, weather was exceptionally severe; on the ninth and tenth the worst sleet storm in twelve years occurred. Sleet fell in small granules, while the temperature remained several degrees below freezing. Partial thawing on January 12, 13 and 14 was followed by a steady drizzling rain on the fifteenth. On the following day the temperature dropped to —7°F. Ice still remained from the sleet storm, and the slush again froze. On the night of January 18, there was one of the worst snow storms on record and temperature reached a low of 2°F. Exceptionally low temperatures persisted through January 24, with more sleet on January 25. Ice from the earlier storm still remained. On January 30, the temperature dropped to —7° and a three-inch cover of snow still remained over the coat of ice. The month of January, 1949, had the heaviest precipitation in 81 years (5.09 inches) and a cover of ice remained for at least 21 days. There were other sleet storms of lesser proportions on February 2 and again on February 21.

Ordinarily sleet would not seriously damage woodrats living in houses in woodland habitats and less suitable hedge rows because it usually freezes as it falls and coats only the surface of the house. Gradual thawing would allow normal runoff without much penetration. Because the sleet during the storm described above did not form a glaze as it fell, the ice particles penetrated many houses. It has been observed many times that captive woodrats refused food that was frozen or were unable to eat it. Woodrats in live-traps in winter rapidly weaken unless a large supply of food is available. If food supplies became sealed over by ice, woodrats would have died by starvation or by falling an easy prey to predators. The rats were more accessible to several predators than were smaller mammals such as meadow voles which were difficult to obtain because of the coating of ice over the fields.

The decimated population surviving into the breeding season of 1949 failed to make substantial gains. In fact, during the following four-year period the general trend of the population over the Reservation as a whole seemed to be one of gradual further decline.

In November, 1949, the rats were almost gone from the area of north slope and hilltop in oak-hickory-elm woodland where the most intensive live-trapping and other field work had been done the previous year. The following descriptions of houses remaining on the area at that time give some idea of the habitat, and of the course of events correlated with the fluctuations in numbers of woodrats.

No. 1. At the hilltop outcrop, partly on a substrate of limestone boulders, built around an elm of two-foot DBH, which lent support to one side. A hackberry sapling one inch in stem diameter grew through the middle of the house, providing further support. The house was two feet high and six feet in diameter, and was in obvious disrepair, with a hole several inches in diameter in its top. It had been occupied in the autumn of 1948. It was constructed mainly of sticks, ranging in diameter from approximately one inch to straw size. Many of the sticks, from .4 to .5 inches in diameter and one to two feet long, seemingly would have been heavy burdens for a rat, although they were of light-weight wood, sumac and elm. Mixed with the sticks were quantities of dry leaves, bark, and chips of wood, all material appearing old and weathered. This house was in elm-oak-hickory woods 50 feet from a culti-

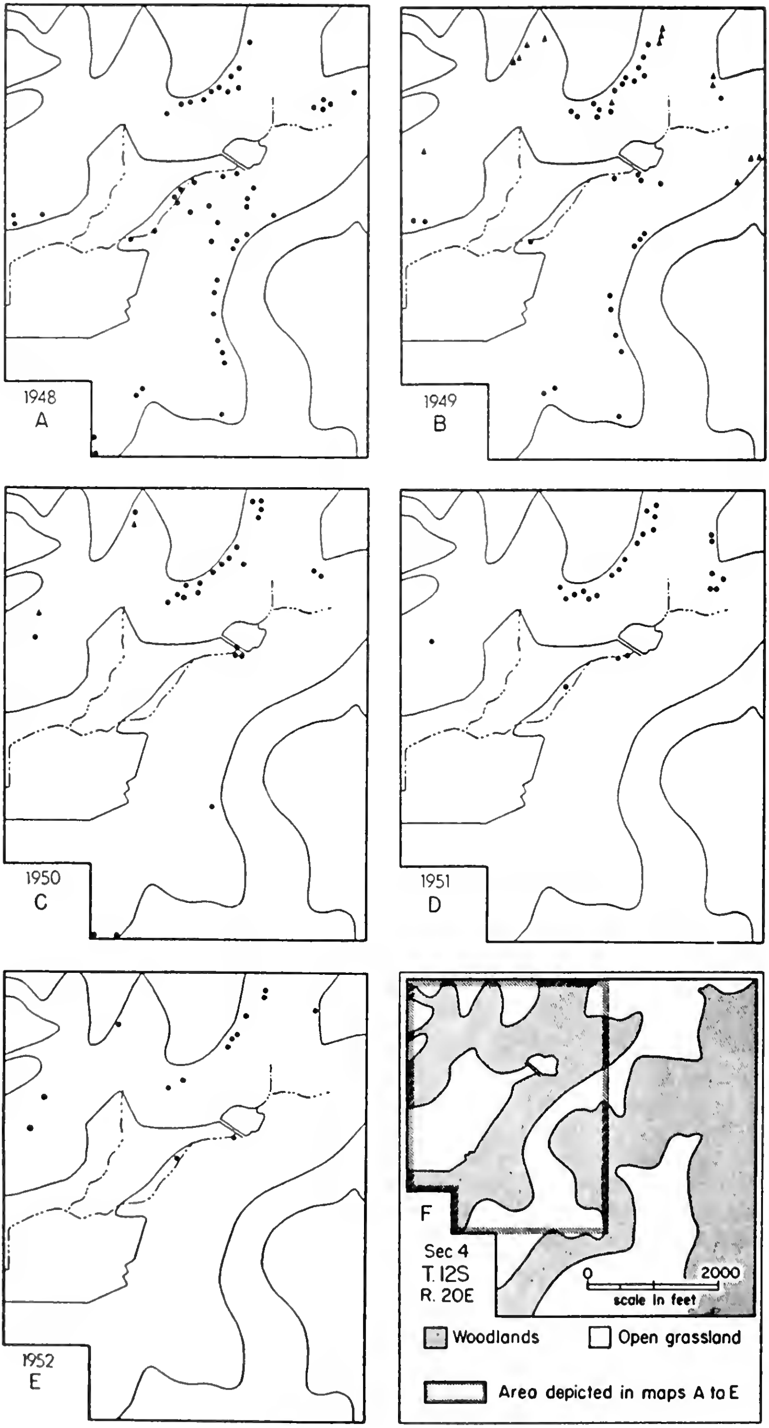
1948
A
1949
B
1950
C
1951
D
1952
E
F
Sec 4
T. 12S
R. 20E
0
2000
scale in feet
Woodlands
Open grassland
Area depicted in maps A to E

FIGURE 1

(A) Map of part of University of Kansas Natural History Reservation, showing first-capture sites for all woodrats live-trapped in the autumn of 1948. Because of the short time involved and the few traps available, much of the area shown was not thoroughly trapped. Woodrats were abundant, though much less so than in 1947, as shown by the large number of deserted houses.

(B) Map of woodrat study area, same as shown in (A), showing first-capture sites for all woodrats live-trapped in 1949. Woodrats were still moderately abundant, but much below the level of the previous year. Triangles indicate those capture sites not sampled in 1948.

(C) Map of woodrat study area, same as shown in (A), showing first-capture sites for all woodrats live-trapped in 1950. Numbers were medium-low, having undergone drastic reduction from the peak level. Triangles indicate those capture sites where trapping was not done in earlier years.

(D) Map of woodrat study area, same as shown in (A), showing first-capture sites for all woodrats live-trapped in 1951. The population was low, but had not yet reached its lowest ebb.

(E) Map of woodrat study area, same as shown in (A), showing first-capture sites for all woodrats live-trapped in 1952, when the population had declined to relatively low numbers and disappeared from much of its former habitat.

(F) Map of the 590-acre Natural History Reservation, showing the area where woodrats were studied.

vated field on the hilltop to the east and south. To the north and west the escarpment sloped away abruptly. There was a coralberry thicket beneath the trees on the adjacent hilltop.

No. 2. On gently sloping hilltop edge 15 feet from the outcrop and escarpment, built around a forked walnut sapling having both trunks approximately five inches in diameter. The sapling, coming up through the center of the house at a 45° angle, evidently had been bent by the accumulated weight of the debris at an early stage of its growth, many years before. Trees were small in this part of the woods, with a well developed understory thicket of coralberry and sumac. This house approximately one foot high and six feet wide, was constructed mainly of sticks and was similar in composition to No. 1, but appeared considerably older with all the sticks blackened and rotten. In the autumn of 1948 this house was used by woodrats, but probably only as a temporary stopping place, because it was already in disrepair then.

No. 3. At edge of escarpment, 25 feet from No. 2, on a flat boulder approximately six feet long, three feet wide and one foot thick. The decaying and much flattened mass of sticks was mainly on top of the boulder, but also spilled over its edges. Fresh sign was noted at this house in the autumn of 1948, but the house was already in disrepair then, and seemingly it was used only as a stopping place.

No. 4. At the hilltop outcrop where an elm had fallen across it. The decaying log remaining was approximately 12 feet long and 15 inches thick. This log passed diagonally through the house, providing its main support. The house was approximately 39 inches high, its summit extending a little above the level of the top of the outcrop. The house was approximately seven feet wide along the outcrop. This house was somewhat intermediate between the typical dome-shaped stick piles that the rat builds in open situations and the formless accumulations of sticks with which some rats living in deep rock crevices line the entrances. Part of the accumulation was beneath the limestone boulders and outcropping slabs. Approximately half of the material used in the house consisted of sticks and the remainder of pieces of bark and chips of wood, mostly gathered from the fallen elm. This house had shrunken noticeably from decay and settling in the months since it was occupied, in the autumn of 1948. The house was surrounded by a thicket of fragrant sumac, dogwood, and hackberry saplings.

No. 5. At edge of a protruding boulder one foot thick at the hilltop outcrop of the west facing escarpment, and 100 feet back in the woods from the edge of a corn field, in undergrowth of dogwood, wild currant, and coralberry. The house consisted of a pile of rotten twigs, 3 inches deep and 30 inches wide on the upper side of the boulder, and a lining of similar material at the lower edge of the boulder, partly blocking the crevice beneath it. The twigs composing the house were old and rotten. However, a few dry but still green hackberry leaves were stored in the crevice beneath the boulder. In a bare space atop the boulder were several recent woodrat droppings, small and obviously produced by an immature individual, which, perhaps, had recently settled at this old house site.

No. 6. In hilltop woods, 30 feet from a corner adjoining a pasture and a corn field, at the base of an osage orange tree of one foot DBH, and also over a hollow cottonwood log one foot in diameter and three feet from the osage orange tree. Suspended mats of grape and smilax vines, and the thorny, dead, lower branches of the tree provided additional shelter. The house was composed of sticks and twigs, mostly of osage orange, with spines still present; slabs of bark, wood chips, and dry leaves also made up part of it. Materials on the exterior of the house appeared old and weathered, but the house was conical and solid. Seven fresh corn cobs were on the house or near its base, suggesting that corn from the nearby field had figured importantly in the diet of the occupant. A well beaten path led from the base of the house alongside the log, to a large cottonwood tree 15 feet from the house. This evidence that the house was occupied was verified by live-trapping the occupant. Late in 1948, also, the house was occupied by another individual, but seemingly was deserted for a period of months thereafter.

No. 7. On upper part of north slope where a hickory seven inches in diameter had fallen across an old sunken log approximately one foot in diameter. The house, composed mainly of hickory twigs ¼-inch to ½-inch in diameter, mixed with bark, wood chips, and leaves, was partly decayed, with no fresh sign and was in a thicket of greenbrier, saplings of hickory and hackberry, and cut tops of hickories. The top was flattened to less than four inches above the level of the supporting hickory log. There were large cavities in the side of the house. When first discovered in the autumn of 1948, this house was occupied by a subadult female rat, but she moved away permanently, and the house had been deserted for approximately a year when these observations were recorded.

No. 8. In middle of northwest slope, in thick branches of broken top of a black oak. This house had become flattened by decay and settling to form a mound approximately one foot high and five feet in diameter. Only the top protruded through the carpet of dry leaves. Once well protected and partly concealed by the branches and twigs of the oak top, this house was now fully exposed by the disintegration of the top. The house consisted chiefly of oak twigs. In October, 1948, a woodrat was live-trapped at this house, but probably it was a wanderer. The house had then already undergone much deterioration.

Natural Enemies

Some 56 species of animals that regularly prey on small vertebrates live on the Reservation. Many of the larger kinds may take woodrats occasionally. Because of size, habitat preferences and the time and manner of hunting, five species stand out as the more formidable enemies—the horned owl (*Bubo virginianus*), prairie spotted skunk (*Spilogale putorius*), long-tailed weasel (*Mustela frenata*), pilot black snake (*Elaphe obsoleta*) and timber rattlesnake (*Crotalus horridus*).

Throughout the study horned owls were common on the area, but their numbers were highest in 1948. Samples of pellet collections have shown that the cottontail is the staple food, being represented in almost every pellet. Various rodents also are important in the diet, the cotton rat, prairie vole, or white-footed mouse being most prominent according to the time and place of collection. The woodrat is approximately optimum size for prey, and it constitutes one of the most preferred food sources. Remains of only two woodrats were found in the pellets examined, but at times when the pellets were collected woodrats were so scarce that they constituted only an insignificant percentage of the biomass of potential prey. On several occasions woodrats in live-traps were attacked by horned owls, as shown by the overturned and displaced trap and quantities of fine down adhering to them and to nearby objects. The horned owl lives in the same habitat as does the woodrat. In other regions woodrats are known to figure prominently in the diet of the horned owl. At the San Joaquin Experimental Range in California, for instance, *N. fuscipes* was found 240 times, more frequently than any other kind of prey, in 654 pellets of the horned owl, and this owl was shown to be the one most important natural enemy of the rat, although many kinds of carnivores, raptors and snakes also took toll from its populations. On the Reservation the population of horned owls has been fairly stable from year to year, with roughly one pair to 100 acres of woodland. Some territories have been maintained continuously throughout the eight-year period of observation, though changing to some extent in size, shape and area included. In 1948, when livestock grazed on the area, and the ground cover of herbaceous vegetation was relatively sparse, cottontails were much less abundant than they were later when the vegetation was protected. Small rodents including voles, cottonrats, and deer mice, were also less abundant then, and the numerous horned owls may have been supported in part by the high population of woodrats.

The spotted skunk may be an even more important enemy of the woodrat, although the evidence is circumstantial. No records of these skunks preying on woodrats have been found in the literature, nor were any such instances recorded by us except for attacks on woodrats confined in live-traps. This skunk is a formidable enemy of small and medium-sized rodents, as it can climb, dig, and squeeze through small openings. That it may prey on rat-sized rodents and may even be a limiting factor to their occurrence is well shown by Crabb's (1941: 353) studies in Iowa. He found that Norway rats (*Rattus norvegicus*) ranked third in frequency (cottontail, mostly carrion, ranked first) in the winter food of the spotted skunk. Crabb observed that about farmyards and farm buildings where the skunks had been eliminated by persistent persecution, rats were abundant, but that about others where the skunks were present, the rats were scarce or absent. On several occasions he noted that heavy populations of rats about farm buildings in summer and autumn nearly disappeared in winter if a skunk was in residence.

Sign of spotted skunk was noted frequently on various parts of the Reservation, especially along the hilltop ledges which were the best woodrat habitat. On several occasions skunks released from live-traps took shelter in woodrat houses which appeared to be unoccupied. According to a local fur dealer, C. W. Ogle, spotted skunks reached a peak of abundance in Douglas County in the winter of 1947-1948, and many pelts were brought in for sale then. The concentration of skunks may have had detrimental effect on the population of woodrats, especially when extremes of weather had already made conditions critical for them, as in early March, 1948, and in January, 1949, when snow and sleet made their usual food supply unavailable.

The long-tailed weasel is considered to be a potentially important enemy of the woodrat. Weasels have been seen on the Reservation on only a few occasions, but they may be more numerous than these records would indicate. Two were caught at the hilltop outcrop, at different times and places, in funnel traps put out to catch snakes. The weasel seems to prefer this rocky habitat, which is also favored by the woodrat. Because of its ferocity and willingness to attack relatively large prey, and because it is an agile climber and able to squeeze through any openings large enough to accommodate a woodrat, it would seem to be a formidable enemy.

The pilot black snake (*Elaphe obsoleta*) is an important enemy of this woodrat on the Reservation and probably throughout the rat's geographic range except for the extreme western part. Although this snake occurs in every habitat of the Reservation, it has been found most often along rock outcrops of wooded hilltop edges in the type of habitat most favored by the rat. Most often pilot black snakes have attempted to escape into crevices of the outcrop. These snakes are also skillful climbers and often have escaped by climbing out of reach along branches or even vertical tree trunks. On several occasions these snakes have been found on or beside woodrat houses, or have escaped into them. Over a seven-year period 143 pilot black snakes have been recorded, 53 of which were adults.

On September, 1948, a large pilot black snake found basking on a rock ledge, distended by a recent meal, was palped and contained a subadult female woodrat. On June 19, 1953, one of us, approaching a live-trap set under an overhanging rock ledge, saw a four-foot pilot black snake on top of it. The snake struck repeatedly at the rat in this trap, but was unable to reach it. At each stroke the rat would dash about the trap frantically.

These snakes hunt by stealth, and might catch woodrats by entering their nests, or by lying in wait along their runways, but are not quick enough to catch them in actual pursuit. Young in the nest would seem to be especially susceptible to predation by the pilot black snake. These snakes hunt by active prowling, either by night or by day, and much of their food consists of the helpless young of birds and mammals found in the nests. While only well-grown or adult pilot black snakes would be able to swallow an adult woodrat, any but first-year young probably would be able to overcome and swallow the small young. The female woodrat's habit of dragging the young attached to her teats as she flees from the house at any alarm must save many litters from predation by the pilot black snake. First litters of young, born in early March, are already well grown, and past the age of greatest susceptibility to predation before the snakes emerge from hibernation in late April or early May.

The timber rattlesnake is another potentially destructive enemy, but on the Reservation, and throughout much of its original range it is now relatively scarce. The genus *Neotoma* largely coincides in its over-all distribution with the genus *Crotalus*, of the rattlesnakes. For most kinds of woodrats, the larger species of rattlesnakes are among the chief natural enemies.

The timber rattlesnake has habitat preferences similar to those of the eastern woodrat. Of 30 timber rattlesnakes recorded on the Reservation over an eight-year period, all but one were at or near hilltop rock ledges in woodland. The woodrat is probably one of the most important prey species for the timber rattlesnake. Like the woodrat, the rattlesnake is mostly nocturnal in its activity. Unlike the pilot black snake, it hunts by lying in wait, striking prey which comes within range, and waiting for it to die from the venomous bite, rather than by active prowling. Therefore, it is probably less of a hazard to young in the nest than is the pilot black snake. Even young rattlesnakes too small to eat woodrats are potentially dangerous to them, as they may strike and kill any that come within range.

Commensals

Rainey (1956) listed many kinds of small animals that use the houses of the eastern woodrat and live in more or less commensal relationships with these rodents.

A situation unusually favorable for observing woodrats and their associates was discovered on the Reservation where, in July, 1948, two old strips of sheet metal, each covering an area of approximately 25 square feet, were used as shelter by a lactating female with three young. This was on a brushy slope just below an old quarry site. A rock pile and remains of an old rock wall were nearby. Woodrats had carried many sticks back under the metal strips, filling the spaces beneath their edges. There was a nest and a system of runways beneath the strips. In the following seven years this site was seldom deserted for long and was used by a succession of individuals. The strips of metal could be easily raised and then lowered into place with little disturbance. Because the situation was not entirely natural, the findings may not be typical of other rat houses. Animals found over a period of years beneath these metal strips include: several dozen each of the ring-necked snake (*Diadophis punctatus*), five-lined skink (*Eumeces fasciatus*), and ant-eating toad (*Gastrophryne olivacea*); several individuals each of cottontail (*Sylvilagus floridanus*), white-footed mouse (*Peromyscus leucopus*), short-tailed shrew (*Blarina brevicauda*), least shrew (*Cryptotis parva*), American toad (*Bufo americanus*), Great Plains skink (*Eumeces obsoletus*), pilot black snake (*Elaphe obsoleta*); and one each of bull snake (*Pituophis catenifer*), spotted king snake (*Lampropeltis calligaster*), red milk snake (*L. triangulum*), and timber rattlesnake (*Crotalus horridus*). The snakes which were potential predators on the rats seemed to be merely utilizing the shelter in these instances, but they may have been lying in wait for prey there.

Among mammals, the cottontail and the white-footed mouse are the most persistent users of the woodrat houses, especially those that are no longer occupied by the rats. On one occasion five white-footed mice were caught simultaneously in a trap set beside a house at the base of an osage orange tree. Subsequent trapping showed that this house was no longer occupied by a rat, but that the mice lived in it. Occupancy of such an old woodrat house by white-footed mice may continue long after abandonment of the house by the rat, even after the house has partly decayed and settled to a small part of its original volume.

Cottontails often have their forms under the edges of houses, either occupied or deserted. These situations offer protection overhead and on three sides. Abandoned houses having one or more of the entrance holes enlarged, as by predators breaking through the side of the house to gain access to the nest, are especially well adapted for occupancy by the cottontail. The rabbit may make its form inside the house structure.

The opossum, also, finds the type of shelter that it requires in abandoned houses that have had the entrances sufficiently enlarged. On various occasions opossums or their remains have been found in such old houses, and opossums released from live-traps have been known to seek shelter in abandoned woodrat houses.

At the old quarry on the Reservation woodrat sign was especially abundant. A wooden bin approximately seven feet square, used to store crushed rock before quarrying operations were abandoned, was inhabited by one rat. At the base of a rock crusher on the top of a bank a few yards from the bin was an accumulation of sticks and other debris brought by woodrats. A rock wall at the top of the bank between the crusher and the bin had many crevices providing shelter for the rats, and projecting rocks were littered with their droppings. In the spring of 1949 the bin and rock crusher were removed, but at least one rat continued to live in the rock wall. In the summer of 1951 several tons of corn ruined in the flood were dumped on the top of the bank above the wall. By autumn, Norway rats, either brought in with the corn or attracted by it, had taken possession of the wall, evidently displacing the woodrats, which were no longer present. Although this Old World murid rat is much different from the woodrat in habits, it seemingly can compete with it and replace it where habitat conditions are otherwise favorable for both.

Movements

The woodrat is dependent on the stick houses that it constructs for shelter. For each individual the house constitutes a home base to which it is attached, and about which its movements revolve. The area within which routine daily movements are confined constitutes the home range, which is variable in size and shape. An individual may, and usually does, alter its home range over periods of time. The home range is somewhat nebulous because the rat may at any time move far beyond the small area to which its activities are largely confined. It may be motivated by sexual urge or other voluntary wandering; it may be enticed by a food supply or some other specific attraction not available near its house; or it may be forcibly displaced by an intruder or may abandon in favor of an offspring.

An occupied house normally has several runways radiating from it. These are well worn paths, smoothed by use, and cleared of obstructions, and the rat tends to keep to them in its foraging expeditions. Usually a trail leads to a bush or tree showing evidence of heavy use by the rat. Ordinarily such a trail cannot be traced more than 30 feet from the house, and it seems that the most concentrated foraging occurs within this short radius. Experience in live-trapping has indicated that the distance covered by a woodrat in its normal foraging for food is ordinarily less than 75 feet in any direction from the house.

Usually the rats can be caught in traps only at their houses or nearby places that they frequent, as indicated by their sign. When travelling, woodrats make use of overhead cover as much as possible. Storing of food seems to be associated with the animal's reluctance to wander far from home. When a rat is gathering preferred food for storage the home range may be enlarged (or the animal may travel beyond the limits of its regular home range). In any case the rat may find it necessary to traverse an additional area in order to reach the food source. This may involve, in part, extension vertically, as when the rat obtains food from trees directly over the house. The home range is thus somewhat three-dimensional; both trails and feeding places are often above ground. Because of dependency on cover, woodrats do not forage randomly in all directions from the house.

Although the house and its immediate environs are defended as a territory by the occupant, possession may be soon relinquished. A woodrat may shift frequently from one house to another, especially if unoccupied houses are readily available. Because woodrats had undergone drastic reduction in numbers, as discussed on p. 505, unoccupied houses in various stages of disrepair were numerous throughout the woodland in 1948 and 1949, and the rats that were present then seemed especially inclined to wander. Even old houses that are collapsed and disintegrating may be used temporarily, or may be taken over and repaired. Houses that are in sites exceptionally favorable in that they provide food and shelter may be occupied more or less permanently, with a succession of woodrats over many generations.

Shifts to new areas are perhaps most often motivated by a search for mates. Such shifts are, on the average, longer and more frequent in males. Males must range farther in search of females when numbers are low. On the other hand, when numbers are high and most of the best sites are occupied, newly independent young and displaced adults are forced to travel greater distances in search of homes. Some of the larger and more powerful males move far greater distances than smaller males. The longest distances recorded were mostly for large adult males in breeding condition. The average maximum distance between successive points of capture for 27 adult males was 345 feet. For 39 females (adults and subadults) the corresponding figure was 143 feet. The extremes for males were 0 to 1080 feet and for females, 0 to 650 feet. Of the 27 males, five moved the maximum distance in a single night. Most of the long movements by males did not constitute clear-cut shifts in home range, and many returned to their original locations.

The average distance between points of first and last captures for 72 subadult and adult males was 165 feet. A similar figure for 72 subadult and adult females was 133 feet. Of the males 23.7 per cent were at the same place at the first and last captures; for females the percentage was 36.1. These figures are from the combined data of our trapping records, but the trends differed sharply in the two sets of records. In Fitch's records, movements averaged longer and difference between the sexes was much less: 189 feet for 41 males and 178 feet for 42 females. Corresponding figures from Rainey's records were: 141 feet for 31 males and 74 feet for 30 females. In Fitch's field work, opportunities to record exceptionally long movements obviously were better because the trap line encompassed a larger area, approximately half a square mile, whereas Rainey's live-trapping was concentrated on relatively small areas. The reason for the greater vagility of females in Fitch's records is less evident. However, the data were obtained within the period of drastic population reduction, at a time when there were numerous empty houses throughout the woodland, facilitating travel, and shifts from one home range to another where conditions were, temporarily at least, more favorable. Rainey found that the females in the small colony in woodland where he trapped, moved much less than did those that lived along the hilltop outcrop, which provided a natural travel route.

Following are several examples of males and females with long histories showing individual variation in frequency and distance of movements.

Males

(1.) First captured October 14, 1951, and last captured 327 days later on September 6, 1952. He was taken 12 times. For the first seven captures (October 14, 1951, to July 15, 1952), no movements were recorded. In the following seven days he moved 367 feet. Within the next 21 days he returned to within 114 feet of the site of original capture. Less than one month later he was caught for the last time, at this same site.

(2.) This large male was captured twelve times over a period of 827 days (March 16, 1952, to June 21, 1954). He tended to wander more than other males and was absent from the trapping area from early 1952 to May 1953. One round trip made in a two-weeks period, amounted to a linear distance of 1894 feet if the rat followed natural cover. The return trip of 947 feet was the greatest distance traversed in a single night in any of the woodrats we recorded. Other movements between successive captures were: 722, 397, 356, 293, 253 and 144 feet (the latter shift made three different times). Sexual urge probably motivated most of his wandering, since numbers of females were low.

(3.) For this male the span of records was 143 days, with 18 captures. For the first eight recaptures, extending over a period of 39 days, he was still at the original location. Four days later he had moved 120 feet and was visiting a female. A week later he returned. In the following month he was recorded as making two more moves, of 115 feet and 215 feet. He was last recorded at the hilltop outcrop.

(4.) The records of this male extended over 465 days, with 13 captures. For the entire period only one movement, of 163 feet, was recorded. Twelve of the 13 captures were at the same house.

(5.) This male was captured 16 times over a span of 130 days. After the second capture he moved 144 feet along the outcrop and was caught there for the next 14 times, having developed a "trap habit."

(6.) This male was in the area 210 days (13 captures) and shifted his range. He was first captured on August 17, 1952, at a house at the rock fence 433 feet from the outcrop. Between this date and October 12, 1952, he moved to the outcrop and established residence in a vacant house. He was recorded as making six more moves, the longest of which was only 40 feet.

(7.) This male was first caught in June, 1949, as a juvenile probably between two and three months old (weighing 96 grams) and hence probably still at the maternal house. In September, grown to adult size, he was caught twice, still at this same place. In October, November, December, and in February, 1950, he was caught 11 times at eight places all within a 90-foot radius of his original location. In April, 1950, he was caught at points 550 feet WSW and 700 feet SW. In October he was caught within 150 feet of the original location. In November, 1950, and in March and April, 1951, he was caught four times at a place 900 feet SW from his original location.

(8.) This subadult male was first caught at the hilltop outcrop on October 4, 1949. Two days later he had moved 160 feet north along the outcrop. A month later he had shifted 600 feet south; in three more days 1040 feet north. On November 15 he was 105 feet south of the November 8 location; on November 16, he had moved 70 feet north. On November 17 he had moved 900 feet back south, but had returned on the 18th to the November 16 location. On

November 22, he had again shifted 900 feet south. All capture sites were at the hilltop outcrop.

(9.) This male was caught as a juvenile (75 grams) on October 8, 1950. On November 9 he had moved 220 feet, from the lower outcrop to the upper, and he was recaptured at or near this same site on November 10, 28 and 29, and on January 11 and February 9, 1951. On November 21, 1951, grown to maximum adult size, he was caught at a new location 1080 feet from the original.

(10.) This male was caught as a subadult twice at the same place on November 30 and December 14. By the following autumn he had shifted to a new location 180 feet south along the outcrop, and he was caught there on September 22 and October 18, 1951, and on January 20 and February 2, 1952.

Females

(11.) This female was captured 27 times over a span of 211 days. She moved back and forth considerably between two houses 40 feet apart but made only one substantial movement of 245 feet; at this time she was in breeding condition. Nearly seven months after the first capture she was seen for the last time only 16 feet from the original site of capture. It was assumed she fell prey to spotted skunks which were raiding traps.

(12.) First captured on March 24, 1951, she remained on the area 105 days in which period she was live-trapped 25 times. Sixty per cent of the total captures were at the same house and the longest movement recorded was only 56 feet. She was last caught in a trap 25 feet from the site of original capture.

(13.) This young adult remained at her house at the rock fence approximately four months. In this period she was captured 11 times. On March 16, 1952, she had moved 410 feet to a house at the eastern section of outcrop, probably searching for a male. She was never seen again.

(14.) This subadult female moved from the site of original capture to a house 253 feet away on the same outcrop. She was probably in search of a new home when caught the first time. She was recorded at another house 40 feet away on one occasion.

(15.) Over a span of 90 days and 15 captures this female was not recorded as making any movement. She was living in one of the woodland houses. Mature males were numerous in the area and she was visited by at least two.

(16.) This female was also living in the woodland section and was first caught on March 30, 1952, in one of the less favorable houses. She was trapped 17 times over a period of 85 days. One movement of 68 feet to a new home site was recorded, but the area of foraging probably did not change. She was caught here four times and then disappeared.

(17.) This female was first trapped as a subadult on October 5, 1948, at a house in brush on the upper part of a north slope. On November 24 she had shifted 590 feet to the bottom of the slope and was living in the recess beneath an undermined honey locust on a gully bank. On November 25 she was caught in a similar situation 100 feet farther east along the gully bank. She was recaptured at the gully on November 26 and 30, December 1, 3, 22, and March 8 and 9, and in all she shifted six times between the two gully-bank dens.

(18.) This female was first trapped as an adult on November 18, 1948, in a gully-bank den. She was recaptured at this same place a year later, on November 18 and 30, 1949. On February 19, 1950, she was caught at a hollow sycamore 650 feet farther up the gully, and she was recaptured there on February 25 and April 7, and on June 15, 1951. On August 6, 1951, she was caught at a house in a thicket on the gully bank, between the first and second locations and 150 feet from the latter.

(19.) This female was recorded only twice; on October 15, 1948, she was at a hilltop rock outcrop. On July 14, 1950, she had moved 1480 feet and was living in a rock pile at the base of the slope, near the same hollow sycamore where female No. 18 had been caught.

(20.) This female was first caught as an adult on April 5, 1950, at a large boulder of a hillside rock outcrop. On October 7, 1950, she had shifted 110 feet to a house at an osage orange tree on the hilltop rock outcrop. On November 9 she was back at the first location and on November 28 she had moved 70 feet south along the hillside outcrop. On January 11 and February 9, 1951, she was back at the original location. On November 9, and 21, 1951, she was again at the site 70 feet south, and was still there at her last capture on February 3, 1952.

Ordinarily each house that is in use harbors only a single woodrat. To a greater degree than any other kind of mammal on this area woodrats show intraspecific intolerance. On various occasions when captives were placed in the same or adjacent cages, they focused their attention on each other with evident hostility, the more powerful or aggressive individuals attacking or pursuing. Several times the confinement of two rats in the same live-trap or cage resulted in the death of the weaker individual, and seemingly this is the normal outcome unless the attacked rat is able to escape. On various other occasions two or more rats have been caught in the same trap simultaneously but in every instance these were either: a pair of adults, the female appearing to be in oestrus; a lactating female and one or more of her young; or young less than half-grown, that were obviously litter mates. Older woodrats, especially males, often have their ears torn and punctured from fighting.

Territoriality involves, primarily, defense of the house itself. An individual that ventures into an occupied house may be quickly routed by the occupant even though the latter is smaller. Chasing has been observed occasionally, but it is doubtful whether any individual is able consistently to defend the entire area over which it forages. Because each rat spends most of its time within the shelter of its house, an intruder might venture onto its home range unchallenged and undetected, so long as it did not enter the nest cavity.

An adult female was live-trapped on October 14, 1951, beside her house at the outcrop. As soon as she was released, she disappeared within the house. After approximately two minutes, a soft, high pitched whine was heard and immediately another woodrat dashed into view closely followed by the female. The chase continued for several seconds in the vicinity of the house, but the woodrat being chased soon left the area *via* the outcrop. Probably this intruder had moved into the house in the night while the female was in the trap.

On June 17, 1952, an adult male was found in a live-trap set at one of the brush pile houses in the woodland area. This house was occupied by an adult female. He ran into the house after release, and immediately there was a loud squeal. He ran outside and paused under some limbs approximately 15 feet from the house, and remained there for 15 minutes before clipping off an ironweed 12 inches long, which he carried to the house. He did not enter the house but stopped beneath overhanging sticks at the edge, eating leaves from the plant. He made another attempt to enter the house but loud squeals and rustling followed and he returned to the ironweed plant and was still eating when observations were halted. In another instance, squeals and rustling indicated that the occupant and intruder were in combat.

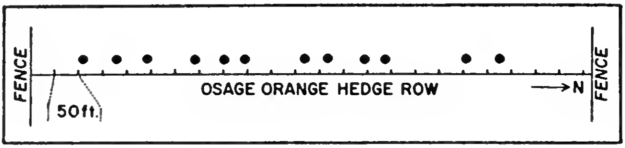

Fig. 2. Diagram illustrating spacing (due to territoriality or intolerance of the rats) in twelve woodrat houses in a hedge row extending south from south boundary of the Reservation at the middle.

Although home ranges may overlap to some extent, intraspecific intolerance tends to maintain a certain minimum interval between houses. The arrangement of twelve houses along a hedge row 1170 feet long is diagrammatically represented in Figure 2. The average interval was 78.5 feet (minimum 42; maximum 171). The habitat was uniform. Home ranges probably overlap somewhat, and the spacing is the expression of the need for an otherwise unoccupied area in which there is sufficient space to live. Because individuals tend to fight whenever they meet, there is probably a psychological tendency for sequestration which results in spacing of houses and reduces social contact thereby avoiding a depletion of energy that would be detrimental to the population. Whereas condition of the hedge row determines whether or not it will be inhabited by woodrats, length determines the number of occupants. The spacing of houses in a hedge row must be attributed to something other than restriction of sites because the number of sites available always exceeds the number that are in use. Although rock outcrops situated in areas of uniform habitat have not been observed to the extent that hedge rows have, a similar spacing seems to exist and the sites available for houses always exceed the actual number found. This behavior pattern limits the number of houses and is probably advantageous to the species through preventing overcrowding and possible critical depletion of the food supply.

Eleven of the young that weighed 100 grams or less when originally captured and were presumably still living at the mothers' houses, were recaptured repeatedly over periods of weeks or months, providing a limited amount of information regarding dispersal. They followed no definite pattern. In seven instances (five males and two females) the young stayed on at the house beyond the age when they were completely independent of the female. In at least two instances the female was known to have moved away while the young remained. One female shifted to a house 58 feet from the one where she had reared her litter of two, and was accompanied by the young male, while the young female stayed on in possession of the maternal house. Two months later this young female was caught at a house 90 feet away, and an adult male was in possession of her former house. One young male shifted to a house 220 feet from his original home and remained there several months, but was recaptured once back at the original location. Another male made a series of moves over a period of weeks and finally settled in a house 490 feet from his first home. One male who stayed in the maternal house all summer, and reached adult size there, later moved several times, and was last recorded 900 feet away. One young female shifted 110 feet. In several instances juveniles appeared abruptly in houses known to have been unoccupied previously, and some of these houses were in poor repair. These young had wandered from their maternal houses, for unknown reasons. On one occasion a young woodrat was caught in a mouse trap set in a meadow, a habitat into which adult woodrats would scarcely be expected to venture.

Feeding

Rainey (1956) has listed 31 food plants that are used by the woodrat in northeastern Kansas. He has emphasized that each rat usually obtains its food from plants growing in the immediate vicinity of its house, and that individuals thus differ greatly in their feeding, according to the local vegetation. Therefore, with a sufficiently large number of observations, the list of food plants might be greatly expanded, to include most of the local flora, with the exception of the relatively few kinds that have developed strongly repellent properties rendering them unpalatable to herbivores in general.

At the quarry where one or more woodrats usually lived beneath metal strips, as described previously (under the heading of "Commensals"), the situation seemed to be especially favorable, despite the fact that the metal offered no insulation from extremes of heat in summer and cold in winter. Perhaps the rat had an alternative nest among nearby boulders, to use when temperature was unendurable beneath the metal.

The rat itself, the stored food, and other details of its home life, could be observed with a minimum of disturbance by raising one side of the metal strip momentarily, then carefully lowering it into place. The following observations made in the summer and autumn of 1948 give some idea of the range of food plants stored at any one time and the change as the season progresses.

July 12: Bundles of leaves of carrion-flower (*Smilax herbacea*); 15 green pods of honey locust (*Gleditsia triacanthos*) with seeds eaten out; several green fruits of osage orange (*Maclura pomifera*), and several seeds of coffee-tree (*Gymnocladus dioica*).

July 24: Bundles of green leaves of osage orange and carrion-flower; many pods of honey locust.

August 30: Three large clusters of the fruits of pokeberry (*Phytolacca americana*).

October 20: Many small clusters of grapes (*Vitis vulpina*) judged to weigh perhaps one pound in all; several old pods of coffee-tree and a few berries of dogwood (*Cornus Drummondi*) and of pokeberry; a pile of small acorns of chinquapin oak (*Quercus prinoides*); dry seed heads of grass (*Bromus inermis* and *B. japonicus*).

December 22: Many twigs of bittersweet (*Celastrus scandens*) with fruits still attached; several seed heads of sunflower (*Helianthus annuus*); a few acorns of chinquapin oak; fragments of the fruit of osage orange; cured bundles of trefoil (*Desmodium glutinosum*), carrion-flower, and tickle grass (*Panicum capillare*).

Although the eastern woodrat is relatively unspecialized in its feeding habits, a few species of favored food plants probably make up the greater part of its diet. In northeastern Kansas, at present, osage orange probably is by far the most important single species. Despite the fact that its aromatic leaves and fruits are somewhat repellent to insects and some other animals, they are well liked by woodrats, and provide a year-round food supply to those individuals having houses in or near the trees. Honey locust similarly provides thorny shelter for house sites, while the foliage, the seeds, and the bark of twigs and trunks are eaten. In houses that are situated near honey locusts, the large, heavy seed pods are sometimes stored by the hundreds. Old pods are often used in substitution for sticks as building material in the house. Nevertheless, honey locust is used relatively little as compared with osage orange. Other plants that figure most importantly in the diet include bittersweet, fox grape, pokeberry and horse nettle (*Solanum carolinense*).

Rainey (*op. cit.*) mentioned that captive woodrats would eat meat, both cooked and raw, and on one occasion he found remains of a cicada on a house under circumstances suggesting that this insect had been eaten by a rat. In the course of trapping for opossums and small carnivores, woodrats were caught on many occasions by Fitch in traps baited with animal material exclusively—miscellaneous meat scraps, canned dog-food, bacon grease, or carcasses of small vertebrates. In fact, such baits seemed to be even more attractive than the grain, seeds, peanut butter and raisins that had been used customarily to bait the traps set for woodrats. However, such meat baits could be used effectively only in cold weather, because of rapid spoilage and interference by insects at higher temperatures.

On one occasion an adult pilot black snake found dead on the road, a recent traffic victim, was brought to the Reservation headquarters for examination and was left overnight in the garage. On the following morning the carcass of the snake was found to have been dragged a short distance and gnawed; a quantity of flesh was eaten at an exposed wound on the neck. Woodrat tracks were thickly imprinted on the dusty soil around the snake. The adult male woodrat that lived in the garage had evidently spent much time moving about the carcass and over it, and feeding upon it. It seemed remarkable that this individual was not deterred from feeding on the snake by an instinctive fear of one of its chief natural enemies.

Although the eastern woodrat's food consists mostly of vegetation, the strong tendency noted to feed upon flesh when it is available suggests that these rodents may, occasionally at least, prey upon helpless young of small vertebrates that are readily available to them. Nestling birds, either on the ground or in low trees, and young mice in nests that are accessible, might tempt the rat to indulge in predation.

Breeding

Reproductive activity continues to some extent throughout the year except in late autumn and early winter. Presence of a vaginal orifice was used as an indication of sexual activity. In most instances the orifice was not indicative of actual oestrus, as it persisted through the preceding and following stages of an oestrus cycle. In anoestrus the orifice is sealed, the genitalia are reduced in size and the skin in the genital region is white. Immature females, and adults during most of the winter, are in this quiescent condition. Onset of the breeding season in late winter is relatively abrupt, and seemingly is a photoperiodic response. Breeding may begin in late January, and most females are in breeding condition within the first half of February. In oestrus the genitalia are enlarged and discolored and the vaginal orifice is prominent and gaping. By February most females born the previous season have matured, and breeding involves the entire population, except possibly for retarded young and individuals suffering from disease, injury or malnutrition. Rainey (1956) recorded an average of 2.3 young per litter.

Number of litters normally produced in the course of a season by an adult female is unknown, but most mature females examined within the period February to September inclusive were in some stage of the breeding cycle. It is obvious that the females which are successful in rearing their litters produce at least two litters annually, and probably some produce three litters. When entire litters are lost at an early age, to predation, or other causes, productivity is much increased, with perhaps only short intervals between pregnancies.

The smallest female having a vaginal orifice weighed 160 grams, but in most instances somewhat larger size is attained before the onset of oestrus. Judging from the average growth rate of immature females (Fig. 3), most probably attain sexual maturity at an age of five to six months unless this age is reached in the winter period of sexual quiescence. Rainey (*op. cit.*) found no clear cut instances of young maturing in time to breed before their first winter. He concluded, tentatively, that in most instances sexual maturity is not attained until the spring of the year following that in which the rat is born. However, the evidence was inconclusive because few of the young marked survived to maturity. In late summer and early autumn, the latter third of the breeding season, newly matured young of the year, born in early spring, may be the most productive group. Young conceived at the beginning of the breeding season, and born in early March, would normally reach adult size and breeding maturity in August. For example, a young female first caught on June 15, 1951, weighed only 150 grams, but by August 10 she had gained to 220 grams (probably in pregnancy) and had a vaginal orifice. Of 35 adult and subadult females examined by Fitch in October, eleven had a vaginal orifice, the latest on October 18. Of these eleven showing signs of breeding, four at least had not yet produced litters, judging from the undeveloped condition of their mammae, and others that showed evidence of recent lactation probably included young of the year that had bred in August or September. One female gave birth to a litter in a trap on the night of October 6, 1950. Of 32 adult and subadult females recorded by Fitch in November, all were sexually quiescent, with the possible exception of one having a partially open vagina on November 10. All females taken in Decmber, and most of those taken in January, also were sexually quiescent. January 20 was the earliest recorded date for a female with a vaginal orifice. Females examined in February mostly were perforate and many of them appeared to be in oestrus. One female trapped on February 19, 1950, weighed only 140 grams and was still imperforate. Another, weighing 200 grams on February 3, 1952, still was imperforate, but by February 27 she was perforate and appeared to be in oestrus. An adult female that appeared to be in oestrus on February 3, 1952, was imperforate on February 10.

Growth

At birth woodrats weigh approximately 10 grams or a little more. In a litter born in captivity and kept by Rainey, the average gain amounted to a little more than 1.5 grams per day during the first two months, but in the third month it was somewhat less. As this was an unusually large litter, of five young, one more than the female's teats could accommodate, their growth may have been a little less rapid than in most of those under natural conditions. At an age of three months they averaged approximately 120 grams. The three males consistently exceeded the two females.

Young weighing less than 100 grams are rarely caught in live-traps. Four young, all males, first caught at an average weight of 80 grams, gained on the average, 1.39 grams per day over intervals that averaged 44 days. Six other young males first caught while in the weight range of 100 to 149 grams, were recaptured after intervals of 17 to 45 days and they had gained, on the average, .92 grams per day. The corresponding figure for four young females in the same size range was .71 grams per day. In seven young males in the weight range 150 to 250 grams, that were caught after intervals averaging 66 days, the gain in weight amounted to .83 grams per day. In seven females in the range 150 to 199 grams, gains averaged only .68 grams per day. Fully grown females that are not pregnant weigh, most typically, a little less than 250 grams while fully grown adult males average a little more than 300 grams. Growth rate and adult weight both

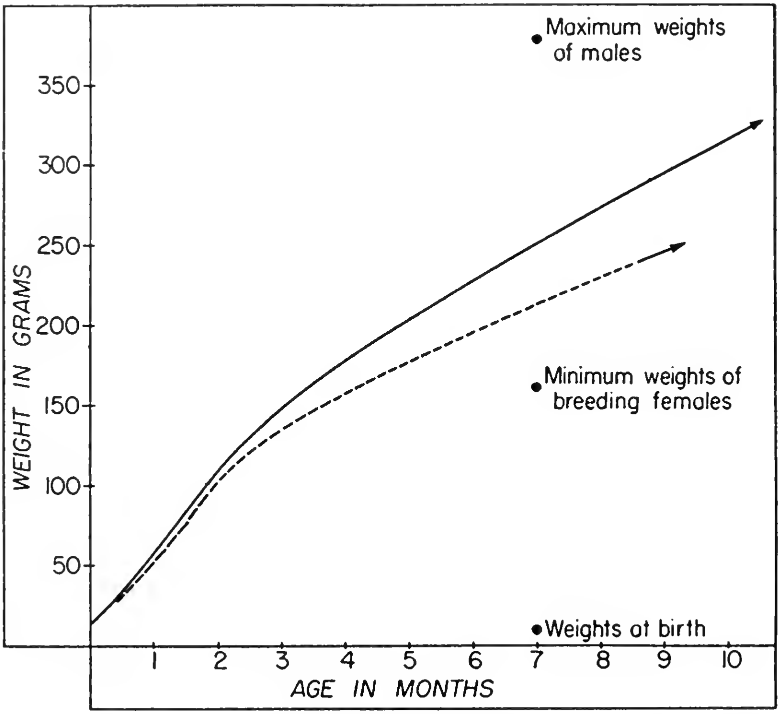

FIG. 3. Typical growth curves for male and female woodrats; early stages are based on the litter of a captive female, later stages on average gains of recaptured juveniles and subadults, excluding those that seemed to be stunted. Solid line represents males and broken line represents females.

are influenced to a large extent by season and even more by individual differences. The underlying causes are obscure in most instances, but individual rats that are still short of adult size may stop growing for periods of months, and some individuals grow much more rapidly than others. One male that weighed 108 grams when he was first caught on July 3, 1951, was estimated to have been born in early May. He was last captured 152 days later on December 2, 1951, and by then his weight was 300 grams, representing an increase of 1.2 grams per day. Another male that weighed only 75 grams when he was caught on October 8, 1950, may have been less than two months old then. By November 21, 1951, at a probable age of 15 months, he weighed 350 grams having attained almost the maximum size. Other exceptionally large individuals were known to be less than two years old, while those rats that survived longest on the study areas did not much exceed average adult size. These records seem to show that exceptionally large woodrats are usually not those of advanced age, but are individuals which have grown most rapidly through fortuitous circumstances, probably depending upon both innate and environmental factors.

None of the woodrats handled was excessively fat, nor were any emaciated. The habit of keeping on hand stores of food at all seasons perhaps obviates the necessity for storing quantities of fat. Seasonal trends in weight vary among individuals, and are not wholly consistent from year to year. Rainey found that in late autumn and winter, rats steadily gain weight reaching a peak in late February or March. However, in the winters of 1948-49 and 1949-50, Fitch found that most rats lost weight and hardly any, even those that were short of adult size, made gains.

The following records of a male born in the spring of 1949 show rapid growth and attainment of adult size in his first summer, cessation of growth during the winter, and resumption of growth, with attainment of near-maximum size the following spring.

June 16, 1949	96 gms.	November 26, 1949	240 gms.
September 26, 1949	230 gms.	November 30, 1949	240 gms.
September 27, 1949	230 gms.	December 20, 1949	260 gms.
October 18, 1949	260 gms.	February 18, 1950	230 gms.
October 27, 1949	250 gms.	April 5, 1950	290 gms.
October 29, 1949	220 gms.	April 7, 1950	300 gms.
November 8, 1949	235 gms.	October 7, 1950	320 gms.
November 15, 1949	245 gms.	November 29, 1950	345 gms.
November 24, 1949	240 gms.	March 23, 1951	340 gms.

Another example, showing winter cessation of growth in a male at even smaller size is shown below. This was in the winter of 1950-1951.

November 9	145 gms.	January 11	175 gms.
November 28	175 gms.	March 1	225 gms.
November 29	165 gms.	March 23	200 gms.
January 10	180 gms.		

Longevity

The longest span of records for an individual woodrat recorded was 991 days in a female, already adult when she was first caught on November 18, 1948. Other relatively long spans of records were: 827 days in a male, adult when first caught on March 16, 1952; 754 days in a female, also adult when first captured; 649 days in a male first captured as a juvenile; 465 days in a male, adult when first captured; 409 days in a male, juvenile when first captured; 399 days in a female, juvenile when first captured; 395 days in a female, adult when first captured; 390 days in a female, adult when first captured; 366 days in a male, adult when first captured. Of these eleven individuals (six females and five males) whose records cover more than a year, eight were already adult when first caught. These eleven rats represent only 4.3 per cent of the total number captured. Our study was made at a time when populations were shrinking and disappearing, and obviously individual spans would have been longer if we had been working with a stable population. In most instances the spans of our records represent only small parts of the life spans of the individuals involved. Nevertheless, our records emphasize the potentially greater longevity of the woodrat as contrasted with the various smaller rodents living in the same area. Of several thousand individuals of the genera *Mus, Zapus, Reithrodontomys, Peromyscus, Sigmodon,* and especially *Microtus,* none is known to have survived so long as two years, and only a few individuals are known to have survived so long as one year after being marked.

Summary

Plant succession resulting from land use practices created habitat conditions especially favorable for woodrats in the late nineteen forties in northeastern Kansas, and particularly on the University of Kansas Natural History Reservation. With protection from prairie fires, woody vegetation had encroached onto areas that were formerly grassland, and, later, fencing against livestock permitted dense thickets of undergrowth to develop. In this region the woodrat usually lives in a forest habitat, and requires for its house sites places that are especially well sheltered, as in matted thickets of undergrowth, root tangles exposed along eroded gully banks, hollow stumps or tree trunks, bases of thorny trees with multiple trunks for support, thick tops of fallen trees, or, especially, rock outcrops with deep crevices.

At the time of their maximum population density in or about 1947, woodrats probably averaged several per acre on the woodland parts of the Reservation. In the autumn of 1948, 17 were caught on the ten-acre tract of woodland that was live-trapped most intensively. By then, however, the population had already undergone drastic reduction, as shown by the fact that there were many unoccupied and disintegrating houses throughout the woodland. While the time and manner of mortality was not definitely determined, circumstantial evidence suggests that the downward trend began in early March, 1948, when record low temperatures and unusually heavy snowfall coincided with the time when parturition normally occurs. The rigorous weather conditions then may have been injurious, not only to the newborn litters but to the females comprising the breeding stock. Nevertheless, the population remained moderately high through 1948, but by early spring of 1949 more than three-fourths of the adults and subadults present in late autumn had been eliminated. Again, unusually severe winter weather seemed to be the underlying cause, as in January precipitation was the heaviest on record in 81 years, with penetrating sleet storms, persistent ice glaze, and occasional brief thawing followed by sudden drops to extremely low temperature.

After the drastic reduction in the winter of 1948-49, the population did not recover. Although no further sudden reductions due to extremes of weather were noted, the trend seemed to be one of gradual, progressive decline throughout the following period of years. Deterioration of the habitat, as the developing forest shaded out undergrowth, and inroads of certain predators may have been important in preventing recovery of the population. Many kinds of predatory mammals, hawks, owls, and snakes probably take woodrats occasionally, but the spotted skunk, long-tailed weasel, horned owl, timber rattlesnake and pilot black snake are considered to be by far the most important predators because of their habits and prey preferences. Few actual records of predation on woodrats were obtained because of their scarcity during most of the period covered by our study.

Of the animals which share the woodrat's habitat, many small mammals, reptiles, amphibians, and invertebrates use its houses and live in a somewhat commensal relationship.

Woodrats are somewhat territorial, each defending its house and an indefinite surrounding area against intrusion by others. Houses tend to be spaced at intervals of at least 40 feet; occasionally they are closer together. Most foraging for food is done within 75 feet of the house. However, woodrats often wander far beyond the limits of the usual home range. On the average, males travel more frequently and more widely than females, and the larger and older males travel more than the smaller and younger. Search for mates provides the chief motivation for wandering. Extent of wandering is controlled to a large degree by availability of natural travelways, such as rock ledges, by shelters for temporary stopping places, such as old deserted houses, and by population density of the rats themselves.

Food of the eastern woodrat consists chiefly of vegetation; many kinds of leaves, fruits, and seeds are eaten. For many individuals foliage and seeds of the osage orange are the staple; hedge rows and dense trees of osage orange provide favorable sites for the houses. Woodrats are attracted to meat baits, and have been known to feed on flesh of carcasses, even on one of the pilot black snake which is a predator on the rat.

Woodrats are born blind, naked, and helpless, at a weight approximately four per cent of the adult female's. They gain at a rate of at least 1.5 grams per day in the first two months. When they have reached a weight of 100 grams, the gain averages somewhat less than one gram per day, but individual variation is great. Males gain more rapidly than females, especially in the later stages of growth, as adult weight is greater by approximately one-fourth in the male. Some individuals grow to maximum adult size at an age of one year. Unusually large individuals are not necessarily those that are unusually old. Longevity is greater in woodrats than in most smaller rodents. One female of adult size when first trapped was last captured 991 days later when she must have been well over three years old, and others are known to have survived more than two years even though populations were shrinking so that few of the rats were able to survive for their normal life span.

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Eastern Woodrat, Neotoma floridana: Life History and Ecology

BY

DENNIS G. RAINEY

UNIVERSITY OF KANSAS
LAWRENCE
1956

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- 15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
- 16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.

(Continued on inside of back cover)

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By

Dennis G. Rainey

CONTENTS

PAGE
INTRODUCTION 539
METHODS 540
DESCRIPTION 542
  General 542
  External Measurements 542
  Weights 543
  Color 543
  Posture 544
  Gait 545
HABITAT 545
  General Considerations 545
  Habitat Relations of the Species 547
  Habitat in Eastern Kansas 549
  Study Area 552
  Moisture Requirements 555
  Relation to Heat 555
  Relation to Cold 557
  Relation to Light 559
HOUSES 560
  General Character 560
  Uses 560
  Signs of Occupancy 561
  Structure 561
  Objects Found in Houses 565
  Houses in Hedge Rows 566
  Houses at Rock Outcrops 567
  Houses in Rock Fences 570
  Houses in Woodland 570

PAGE
Miscellaneous Sites 572
Occupancy of Houses 573
FOOD HABITS 575
BEHAVIOR 583
Temperament and Sociability 583
Communication 585
Development of Senses 586
Sanitation 587
Care of Pelage 587
INTERSPECIFIC ASSOCIATIONS 587
General Considerations 587
Parasites 588
Predators 596
Escape Reactions 599
Commensals and Competitors 601
REPRODUCTION AND DEVELOPMENT 604
Season of Breeding 604
Indications of Breeding in Males 605
Indications of Breeding in Females 607
Size and Numbers of Litters 609
Parturition 614
Newborn Young 615
Care of Young 615
Development and Growth 616
Survival of Young 620
CHANGES IN PELAGE 620
MOVEMENTS 623
POPULATIONS 623
Numbers and Ratios on Study Area 623
Populations Trends 626
DISCUSSION 631
Factors Affecting Populations 631
Distributional Patterns and Factors Limiting Dispersal of Populations 632
The Relation of Homeostasis to Survival 637
The Role of the Woodrat in Community Ecology 639
SUMMARY 640
LITERATURE CITED 642

INTRODUCTION

The objectives of the study here reported on were: (1) to ascertain the range of habitat occupied by the eastern woodrat, *Neotoma floridana* (Ord), in eastern Kansas; (2) to study the life history of the species by means of a long term live-trapping program; (3) to determine those factors in the environment which affect survival, and (4) to attempt to discover factors limiting dispersal and occupation of new habitats. My study was done mostly in the field but laboratory investigations were an integral part of it.

Live-trapping was initiated in March, 1951, and terminated in June, 1954. A part of the area chosen for live-trapping is on the University of Kansas Natural History Reservation and the remainder on adjacent privately owned land. The Reservation is a tract of 590 acres set aside in 1948 as a natural area for the preservation and study of plants and animals native to Kansas.

Woodrats were studied taxonomically and results made available in the excellent report by Goldman (1910). Even though many more forms of woodrats have since been discovered and described and distributions more accurately ascertained, a thoroughgoing revisionary study has not been made since that of Goldman, and one is much-needed. Detailed accounts of life histories have been set forth for *N. fuscipes* by Linsdale and Tevis (1951) and for *N. albigula* by Vorhies and Taylor (1940), but little has been published concerning several of the widespread species such as *N. lepida, N. mexicana,* and *N. micropus.* The study by Finley (MS) adds much to knowledge of the ecology of these lesser known species. Species restricted to Mexico are even less known. Numerous reports of somewhat lesser scope dealing with certain phases of life history have been published for other species such as that of Poole (1940) on *N. magister.* Scattered information for most of the species but concerned principally with habitat is to be found in the numerous faunal reports. A thorough study of the life history and ecology of the eastern woodrat has not been made heretofore. Excellent reports by Hamilton (1953), Murphy (1952), and Pearson (1952), are limited in scope. All available literature has been investigated and used in this report whenever pertinent to the discussion.

Woodrats are not commonly seen because of their nocturnal habits, but they are not unfamiliar to the general public. Many stories are told concerning the "trading" propensities of woodrats, or pack rats as they are frequently called. Woodrats are not averse to living in barns, and when they do, they often are confused with the non-native murine rats. The hairy tail, large hairy ears, large eyes, and soft pelage serve to distinguish woodrats from the introduced Old World species of rats.

Woodrats are not of great importance economically in the United States although they are utilized as food in parts of Mexico.

Several persons have been of great assistance throughout the period of study and without their aid this report would have been difficult to complete. Dr. Henry S. Fitch, Resident Investigator of the Reservation, has devoted many arduous hours to counseling, assisting with field problems, and aiding in preparation of this manuscript. His unselfish help is acknowledged with sincerest gratitude. I am grateful to Professor E. Raymond Hall for his encouragement and assistance in critically reading this manuscript and to Professors A. B. Leonard and Rollin H. Baker for valuable suggestions and advice. I would like to express special thanks to the following for identifying ectoparasites: Dr. Richard B. Loomis of Long Beach State College Department of Zoology for identifying the chiggers; Mr. Earle Cross of the University of Kansas Department of Entomology for identifying the fleas; Dr. Curtis Sabrosky of the United States National Museum for identifying the cuterebrid parasite; and Dr. Glen M. Kohls of the Rocky Mountain Laboratory for examining the ticks. I am indebted to all my friends and associates who have aided in various ways and finally, to my wife, Bettye Rainey, for assistance with field work and preparation of this manuscript. All photographs were made by the author.

METHODS

The live-traps used, patterned after those described by Fitch (1950:364-365), were of one-half inch hardware cloth, five inches high, five inches wide, and 20 inches long. Wooden nest boxes were constructed so that they would fit into the rear of the traps which were left open for this purpose. The boxes were soaked with linseed oil and painted on the outside to waterproof them. The inside dimensions of the box were just large enough to accommodate an adult rat. Several traps with large vegetable tins attached to the rear for nest boxes were used later in the field work, but these were not so satisfactory as the former because often they could not be inserted under rock ledges. A few traps without nest boxes were used. They were as efficient as those with nest boxes if placed under a protective ledge of rock (Plate 1). Large wooden rabbit-traps with an outside string as a part of the trigger mechanism proved inefficient because woodrats persisted in removing the string.

In winter, each trap was supplied with enough cotton so that a warm nest could be fashioned by a captive woodrat. The nest box was not large enough to permit making the nest inside, but the captive would pull out the cotton and form the nest on the floor of the trap (Plate 1). A gallon-sized anti-freeze can cut and shaped to form a hood covering the wire part of the trap was effective in preventing rain or snow from reaching the cotton nest (Plate 1). In summer pieces of board wider than the trap were placed on top to provide shade when necessary. Pieces of screen wire were fastened over the bottoms and the sides of the traps posterior to the triggering mechanism to prevent losing bait. Before screen was used, white-footed mice, *Peromyscus leucopus* (Rafinesque), would undermine the trap and remove the bait which had fallen through.

Several kinds of baits were tested. Mixed grain ("chick scratch"), combined with raisins proved to be the bait most consistently acceptable, and most economical. Either meat or raisins alone would attract woodrats, but in summer these baits were unsuccessful because of interference by ants. When mixed with "chick scratch,"

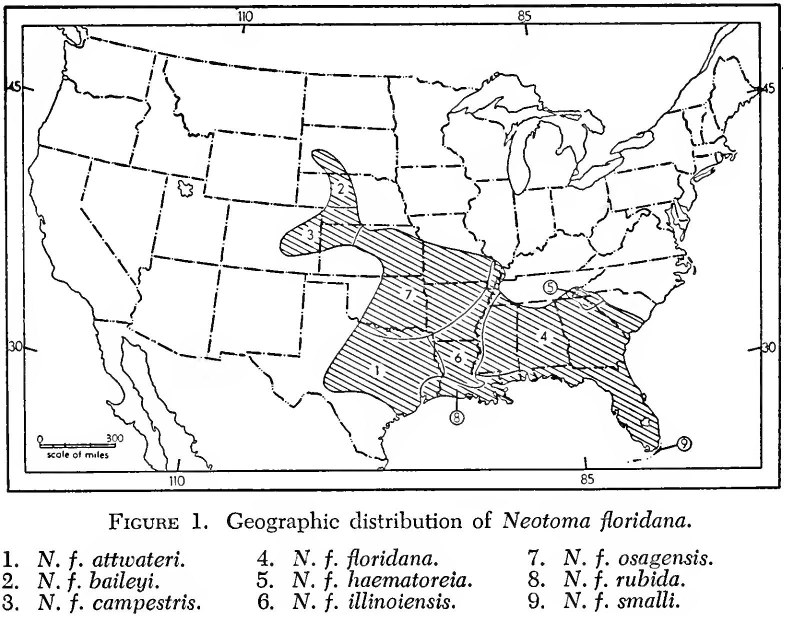


FIGURE 1. Geographic distribution of *Neotoma floridana*.

1. *N. f. attwateri.*
2. *N. f. baileyi.*
3. *N. f. campestris.*
4. *N. f. floridana.*
5. *N. f. haematoreia.*
6. *N. f. illinoiensis.*
7. *N. f. osagensis.*
8. *N. f. rubida.*
9. *N. f. smalli.*

raisins rapidly lost most of their moisture and were then less attractive to ants. A quantity of chick scratch with a few raisins to attract the rat was placed behind the trigger or directly in the nest box. A small amount was scattered in front of the trap.

Live-traps were not placed according to a prescribed pattern. One or more traps were placed at each house and, when trapping at a rock outcrop, I placed additional traps at sites where sign, such as accumulations of droppings, were present. If a trap failed to yield a capture after several nights, it was usually moved. Large rocks were used to anchor the traps to minimize disturbance by predators. The doors of the traps were rigged so that they would lock after being sprung, and some traps were wired firmly to large rocks or to adjacent small trees. However, on many occasions, predators succeeded in opening traps.

DESCRIPTION

General

Like most other members of the genus, this species in external appearance is characterized by large, rounded, and sparsely haired ears; tail covered with short hairs; large black eyes; and soft pelage. The large eyes, which protrude from the head, are characteristic of an animal nocturnal in habits. The toes, four on the front feet and five on the rear feet, have well-developed sharp, downwardly curved claws. Large apical and palmar pads aid in climbing. The vibrissae may extend to a maximum distance of 75 millimeters on either side of the nose. The muzzle is pointed but there is no obvious demarcation between it and the forehead. The body is compact, robust, and highly muscular in large males. The skin is thickened in older individuals of both sexes.

External Measurements

External measurements, in millimeters, of 48 adult specimens, 28 males and 20 females, in the University of Kansas Museum of Natural History indicate that males tend to average slightly larger in total length, length of tail, and length of hind foot. Measurements (total length, length of tail, hind foot, and ear) for 28 males are: 374 (305-450), 160 (130-180), 40 (35-49), and 26 (23-30). Measurements for 20 females are: 369 (300-399), 157 (130-172), 39 (35-42), and 26 (24-29). These specimens, all of the subspecies *osagensis,* were collected in Douglas, Marshall, Ellsworth, Anderson, Greenwood, Jackson, Jefferson, Chase, and Cowley counties, Kansas.

Weights

Males attain greater weights than females. The largest weight recorded for a male on the study area was 384 grams; the next largest weight was 375 grams. Females because of pregnancy and nursing young vary more in weight over periods of time than do males, but the males also fluctuate. Sometimes they suddenly lose weight; for example, an adult male that weighed 365 grams on April 22, 1951, had declined to 290 grams eight days later. Three days later his weight had further declined to only 260 grams, representing a net loss of 105 grams over an eleven-day period. After one month, his weight had increased to 375 grams. In general, adult males tend to reach their peak in weight in February and March at the beginning of breeding season, and decline to their annual low point in May. There is a fairly rapid recovery of the males in June, when most females are having litters. There are other slight declines in July, probably because of extreme hot weather, and in September and October as activity in storing of food increases. In late autumn and winter, weight steadily increases until the peak is again reached.

The average weight of 21 adult males when live-trapped the first time was 299 grams (220-384). The average weight of 23 subadult males when live-trapped the first time was 197.4 grams (130-250). The average weight of 14 non-pregnant adult females was 216 grams (174-260).

Color

The dorsal surface varies from Sayal Brown (capitalized color terms after Ridgway, Color Standards and Color Nomenclature, Washington, D. C., 1912) to Snuff Brown, tinged with black in varying intensities. The black wash is more intense on the back than on the sides and tends to be slightly darker in winter than in summer at which time it varies from Sayal Brown to Clay Color. The dorsal surface in worn summer pelage preceding molt becomes bright Orange-Cinnamon. A lateral line of Pinkish Cinnamon, usually obvious in winter pelage, is indistinct in summer pelage. In winter this color extends over the front legs and under the armpits on the chest but not to the mid-ventral line, and it covers a larger area on the chest in winter than it does in summer. The head is generally the same color as the dorsal surface but becomes grizzled in older animals.

The ventral surface is whitish. Hairs in the pectoral and inguinal regions are usually white to the base; hairs on the sides of the abdomen are plumbeous at their bases. In some individuals the gray cast in the abdominal region is pronounced, while in others, the entire ventral surface appears white and the gray can be seen only by parting the hairs. This is probably due to condition of molt.

Males, according to age and season of the year, usually have a brown stain on the white hairs of the ventral mid-line. Howell (1926:16-17) attributed such a stain in the bushy-tailed woodrat to action of sebaceous glands in the thickened dermal area of the mid-ventral line. He suggested that they functioned as scent glands. Howell (*op. cit.*:214) stated that this glandular area was not present in the representatives of the subgenus *Neotoma* which he studied (*Neotoma albigula albigula* and *Neotoma fuscipes macrotis*). However, Linsdale and Tevis (1951:241) did observe similar brown staining on the dusky-footed woodrat (*N. fuscipes*) and concluded that it was the result of such a glandular area. The stain in *floridana* that presumably also results from a glandular area, becomes more pronounced in older males. It attains a maximum size of one inch in width in the middle of the abdomen and extends from the chest to the anus tapering at either end. The stain generally undergoes a seasonal cycle in intensity. It begins to diminish in August and by October or November, is not pronounced. In February and March, however, individuals are again observed with dark stains. Generally, the greatest extent of staining occurs in June and July. The degree of activity of the glandular area varies considerably between individuals even though all might be old adults. Younger males seldom have intense staining. At least one male that was handled on many occasions did not show the stain. One female was observed with mid-ventral staining similar to that in males.

Hair on the hind feet is white above and slate gray below. The front feet are white, tinged with gray. The tail is sharply bicolor, blackish above, whitish below.

An albino of *osagensis* in the University of Kansas Museum of Natural History (18682 adult female) was obtained four and one-half miles NNE of Welda, Anderson County, Kansas. The pelage is pure white and the collector recorded that it had pink eyes. Melanistic individuals have not been observed.

Posture

When a woodrat is indifferent to its surroundings (see Fig. 3, Pl. 1) the animal rests its weight on its rear feet and sometimes also on the base of the tail. The tail usually extends upward at an angle, but may be straight or arched downward, it may be relaxed resting on the substratum either extended straight or curved. The abdomen usually either touches the substratum or is slightly raised from it. Both of the front feet are generally touching the ground and sometimes the animal maintains a semi-prone position resting on the elbows. The ears are relaxed but not lying flat on the head. When a woodrat is alert to possible danger, the ears are directed forward, and the pupils of the eyes dilate. The entire body is held tense in a "half-crouch" with the weight still on the rear legs and frequently, one front leg is lifted and held flexed across the chest. The tail remains motionless and extended upward. The vibrissae are usually in motion.

Observations on several captive woodrats and of one free-living rat indicated that the most common position when asleep was on the side with the nose between the front legs. The tail may be in a variety of positions, even bent under the body. The pelage is fluffed up and not sleek as when the animal is active.

A woodrat when angered by another frequently lies prone with the head extended forward. The ears are rigid and directed forward even farther than when the animal is alert to possible danger. When the rat fights, the ears are not held flat. This position may account for frequent damage inflicted on the ears. As the rat prepares for combat the vibrissae move rapidly and the tail is flicked quickly from side to side and occasionally strikes the substratum with considerable force.

Gait

When an adult runs, the body is close to the ground and the tail is straight, sometimes held at an angle of as much as 45 degrees and sometimes held parallel to the ground. Juveniles when running, especially if on open ground, move in a series of bounces with the head held low and directed down. The tail may or may not have an upward curve in it. A woodrat seldom moves in a slow methodical fashion, but usually progresses by alternating short pauses with rapid dashes. Even in darkness running at full speed a rat is able to enter an opening scarcely larger than its own body. When a woodrat climbs on a vertical surface such as a tree it seems to rely to some extent on speed and momentum. Woodrats are proficient climbers, but have never been observed to climb by creeping slowly upward as squirrels often do.

HABITAT

General Considerations

The habitat that a woodrat can occupy consists of numerous intricately related environmental factors which function as a unit. To survive the woodrat must withstand extreme environmental fluctuations which might occur only rarely. If one of these environmental conditions is effectively changed beyond the tolerance of the species, this factor becomes limiting and the animal is forced to adapt, move, or perish.

Both physical and biological factors are important in determining suitable habitat for woodrats. The eastern woodrat is most typically an animal of the eastern deciduous forest, although in some areas it occupies habitats more characteristic of other species. *N. floridana* occupies a wider range of habitats than any of the other species of woodrat, which indicates greater plasticity to respond to factors of the environment. With certain exceptions, woodrats are generally associated with arid rocky regions having xerophytic vegetation. The eastern woodrat occurs in this more typical habitat and also in habitats of the opposite extremes.

Being neither strictly arboreal nor fossorial in habits, a woodrat owing to its size is strongly dependent on the presence of abundant cover in its immediate environment. Under most conditions, woodrats compensate to some degree for this need by constructing their characteristic stick houses that serve as a modifying influence on environmental factors such as extremes of temperature and moisture. Morevor, in many cases, overhead cover protecting the house from severe weather conditions is highly important in determining whether or not the house will be occupied by a succession of woodrats. Such continued occupation is the measure of a successful house site. Furthermore, while foraging for food and seeking mates, the woodrat is more vulnerable to predation unless adequate cover is present. The right kind of cover is essential to provide means of escape from enemies. To escape, the woodrat climbs or seeks shelter in a space small enough to prevent the enemy from entering. The house itself provides effective protection from most predators. If the woodrat is to extend its range and occupy niches within limits of tolerance, the migratory routes must have adequate cover. Seemingly, the critical factor is not kind of cover but amount and structure of cover.

For the woodrat to survive it must have an abundant food supply available, but the versatility displayed by woodrats in their feeding habits indicates that in most instances food is not so critical as cover. In the course of this study, many instances were noted in which foods, identical both in kinds and abundance, were present in two nearby areas one of which was occupied while the other was not. The only discernible difference was in the amount of cover.

Factors such as composition and moisture content of the soil and physiographical features frequently determine the suitability of woodrat habitat. Only those rock outcrops having numerous deep fissures and overhanging ledges are preferred home sites. In certain areas where soil types are suitable, woodrats prefer burrows for nest sites.

Where stick houses are built, means of support for their construction must be available. Even though shortage of suitable building materials may be overcome by a few individuals, such shortage would prevent the existence of a stable population. Numerous examples of such limitation were observed where only flimsy weed stems were available as building materials. The structure and amount of cover perhaps are the most important environmental factors.

Habitat Relations of the Species

Generally, the eastern woodrat is associated with dense timbered and swampy areas in the southeastern part of its range and when more xeric conditions prevail in the northwestern part, the rat is found in rocky situations such as caves, outcrops, dry rocky hillsides, and intermittent wooded stream courses with sparse vegetation. The greater part of the geographic range of this species lies in the eastern deciduous forest; however, it extends into the grassland of the Great Plains to the westward. In eastern Colorado at the western limit of the species, it lives under conditions of scanty rainfall where vegetation is mostly of xerophytic type. Here the houses usually are associated with cactus (Warren, 1942:209).

At the southernmost edge of the range at Key Largo, Florida, woodrats (*N. f. smalli* Sherman) build houses on the rocky floor of the hammocks (Sherman, 1955:113). In central Florida, houses of woodrats, *N. f. floridana* (Ord), usually are built under willow trees on high ground in swampy areas (Hamilton, 1953:180). Also in central Florida, Hill (1945:88) observed woodrats in a dense swamp adjacent to a slow running creek. Cypress, bay, and gum were the principal kinds of trees. The swamp was only a few inches above the level of the creek and subjected to periodic flooding. Farther north in Levy County, Florida, Pearson (1952:459) reported that woodrats were most abundant in areas of dense shrubs in the ecotone between high and low hammock situations. Pearson further observed that nests are frequently constructed in subterranean chambers. In north-central Florida, Blair (1935:271) and Worth (1950:423) found these rats associated with timbered and swampy areas. Worth (*loc. cit.*) observed them usually in the vicinity of water and reported their distribution to be sporadic in that area.

In the Okefinokee Swamp in southeastern Georgia, Harper (1927: 356-360) reported that woodrats lived in stands of cypress in the watery prairies. He found houses in hollow trees, logs, and stumps, as well as uninhabited buildings. In southwestern Georgia, Harper (1929:84) stated: "A swamp rat, building nests of sticks in vines or on the ground, was reported, and could be nothing else but this species [*N. f. floridana*]". In the vicinity of Charleston, South Carolina, Chamberlain (1928:152) found the same subspecies in a wooded, swampy area. Houses were constructed either on the ground or in tangles of grape and smilax vines up to heights of 15 feet. Hollow trees were also utilized as home sites. Chamberlain (*op. cit.*:153) also noted that their distribution was sporadic. Howell (1921:52-53) found *N. f. floridana* most frequently in wooded bottoms or swamps. In the Prairie Belt and Tennessee River Valley of Alabama he found them chiefly in osage orange hedge rows where they often constructed houses 10 to 15 feet from the ground. Rocky bluffs and cliffs were inhabited where present, and large houses were not built.

In northwestern South Carolina, Coleman (1949:200) found *N. f. haematoreia* A. H. Howell living among granite rocks blasted out of the mountain side in the construction of a highway along a precipitous ledge.

The subspecies *N. f. rubida* Bangs occupies habitats much the same as does *N. f. floridana.* In marshes of south-central Louisiana, Svihla and Svihla (1933:73-74) found this woodrat living on tree islands of palmetto, live oak, willow, and cypress. Houses were built against fallen logs, bases of trees, and up in trees. Uninhabited buildings were favorite sites when available. In eastern Texas in river bottom and hammock country, Baker (1942:343) collected specimens of this race where vegetation was dominated by stands of hardwood and pine timber with a luxuriant undergrowth of shrubs and vines, and he stated: "Woodrats in this region apparently do not build brush houses. Burrows at the bases of trees were the only type of woodrat dens observed." In studying this same subspecies in Liberty and Hardin counties, Texas, Bailey (1905:107-109) found that it lived in the thickest woods and around deserted buildings. He stated: "No trace of the rats was found except under the protecting cover of dense timber, brush, or vine tangles, or in hollow logs, trees, or old buildings . . . at Houma, Louisiana . . . I found these wood rats common in the woods and swamps. Some of the houses were built at the bases of hollow trees, over old logs, or under thick brush mats, but just as commonly they were placed in the lower branches of trees or in vines 10 to 30 feet from the ground."

The literature contains but little information concerning the habitat of the subspecies, *N. f. illinoiensis* A. H. Howell. Howell (1910:228-229) found this rat inhabiting crevices and caves along the high rocky bluffs of Wolf Lake in southern Illinois. Kellogg (1939:283) thought this woodrat might occur along the bluffs and in swamp bottomlands bordering the Mississippi River in Tennessee.

In the range of the subspecies *N. f. attwateri* Mearns more xeric conditions prevail. Otherwise, the habitat is somewhat similar to those of the other subspecies; often the rat is found along stream courses. In south-central Texas, Lay and Baker (1938:418-421) found *attwateri* using underground dens along wooded stream banks. One individual was living in a burrow made by an armadillo (*Dasypus novemcinctus*). Post oak (*Quercus stellata*) and winged elm (*Ulmus alata*) were the principal trees. In the same area, Strecker (1929:220) had earlier found *attwateri* occupying caves and crevices along wooded stream banks. Farther west, in Kerr County, Texas, Bailey (*op. cit.*:110) states that this subspecies ". . . lives in a rocky half-forested region. It makes its house sometimes among the rocks, piling up its rubbish in a broken cliff, rock piles, or old stone walls, and sometimes in the woods at the base of a tree, under a brush pile, in some old cabin, or along the river in heaps of flood drift."

Habitat in Eastern Kansas

Present habitat of the woodrat in eastern Kansas is divisible into two principal types; the osage orange, *Maclura pomifera* (Raf.), hedge-row habitat type, which is the more widespread, and the rock outcrop type of habitat. Stone fences, upland woods, wooded stream courses, shrubby hillsides, and uninhabited buildings constitute habitat types of less importance.

According to Livingood (1914:3), the original range of the osage orange tree covered little more than 10,000 square miles. Its northern limit was near Atoka, Oklahoma, and its southern limit somewhat south of Dallas, Texas. It extended into northwestern Louisiana and southwestern Arkansas. Its broadest east-west extent, approximately 120 miles, was in Texas. Between 1865 and 1939, 39,400 miles of single-row osage orange hedge rows were planted by farmers in Kansas (Yearbook of Agriculture, 1949:783). The growth habit of this tree, especially as modified by trimming, makes hedge rows excellent habitat for woodrats. Leaves and fruit or "hedge balls" furnish an ample supply of food. As the planted hedge rows matured and the rather rapid destruction of native timber by man took place, woodrats seemingly shifted from wooded stream courses to this more favorable new habitat. In northeastern Kansas, Kellogg (1915:182) found that woodrats preferred living in tangled underbrush in the lowlands along timbered streams. They built houses around hollow logs or under overhanging roots of trees along creek banks. In the course of this study few occupied houses were observed in this situation. Woodland along several streams in Greenwood County in southeastern Kansas was investigated for the presence of woodrats in 1954; none was found although they were numerous in hedge rows of that area. Changes brought about by man in cutting of timber may have unfavorably altered habitat along stream courses.

The presence of a hedge row does not necessarily create conditions favorable for occupancy by woodrats. In eastern Kansas in 1955 unoccupied hedge rows are more numerous than those that are occupied. In some areas, this is not due to absence of woodrats but is the result of the condition of the hedge rows. Farmers frequently trim the trees after they reach a large size, in order to gain additional ground for cultivation of crops. Many farmers destroy the hedge rows because of their tendency to draw water from the soil, even at considerable distances from the row. In an untrimmed row the limbs grow from the trunk close to the ground and bend, arching outward and downward to form a canopy. The growth is so thick and the thorny limbs so formidable that it is usually necessary to remove several limbs before reaching the base of the tree (Fig. 1, Pl. 2). When trees are young, trimming, or browsing by cattle results in a thick bush. Under these influences trees in hedge rows usually have multiple trunks branching close to the ground, well suited to support houses of woodrats. The wood is extremely tough and durable and limbs from these trees last for many years before rotting. Houses constructed in hedge rows are always made mostly from sticks of the osage orange tree. Limbs trimmed by farmers are frequently left in piles providing a source of building material, and on occasion houses are constructed in the brush piles. Many excellent escape routes are available owing to the close proximity of the trees in a hedge row. When a house is disturbed, the rat, in most instances, dashes from the house up into a tree. If pursued further, it can travel with ease from tree to tree. Rats are

PLATE 1

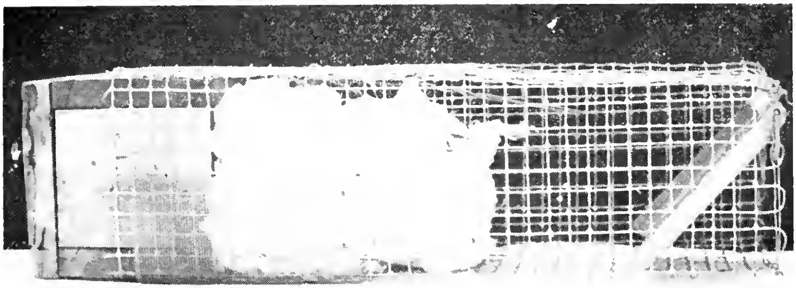


FIG. 1. Live-trap containing wooden nest box. A captured woodrat has pulled cotton from nest box to form a nest. × approx. ⅕.

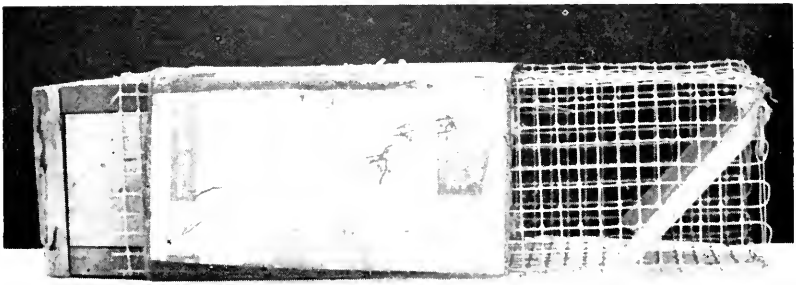


FIG. 2. Metal can around live-trap to provide protection from rain and snow. × approx. ⅕.

FIG. 3. An adult, female, eastern woodrat (raised in captivity—from parents captured 4½ mi. NNE Lawrence, Douglas Co., Kansas), illustrating typical posture when not alarmed. December 4, 1953. × approx. ⅓.

PLATE 2

Fig. 1. A hedge row that has been allowed to grow, providing excellent woodrat habitat, with adequate cover and sites for houses. Jefferson County, July 27, 1954.

Fig. 2. A hedge row 7 mi. E Eureka, Greenwood County, Kansas, supporting a large population of woodrats. Note the lack of ground cover away from the row. Woodrats living here were entirely dependent on the row for food and shelter.

PLATE 3

Fig. 1. An isolated osage orange tree, 6 mi. N Madison, Greenwood County, Kansas. There was a large woodrat house up in the tree, which furnished all essentials for the existence of the woodrat. No other woodrat could be located within a half-mile radius.

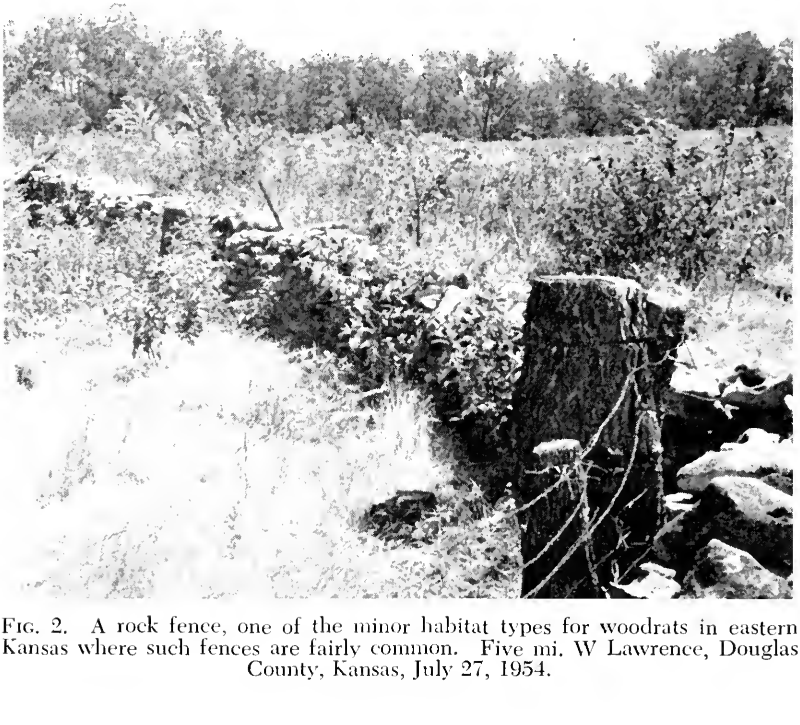


Fig. 2. A rock fence, one of the minor habitat types for woodrats in eastern Kansas where such fences are fairly common. Five mi. W Lawrence, Douglas County, Kansas, July 27, 1954.

PLATE 4

Fig. 1. Tongues of forest along small stream courses in the Flint Hills, 8 mi. S Manhattan, Riley County, Kansas, in terrain dominated by grasses. July 25, 1954.

Fig. 2. Thickets along a stream course in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas, a habitat favorable for woodrats. July 25, 1954.

Fig. 3. Site of woodrat houses in the Flint Hills among limestone boulders of "rimrock" with thickets of dogwood. Wabaunsee County, Kansas, July 25, 1954.

PLATE 5

FIG. 1. One of the smaller houses in the hedge row discussed on page 566. The house was 821 feet south of the southeast corner of the Reservation on private land. November 17, 1954.

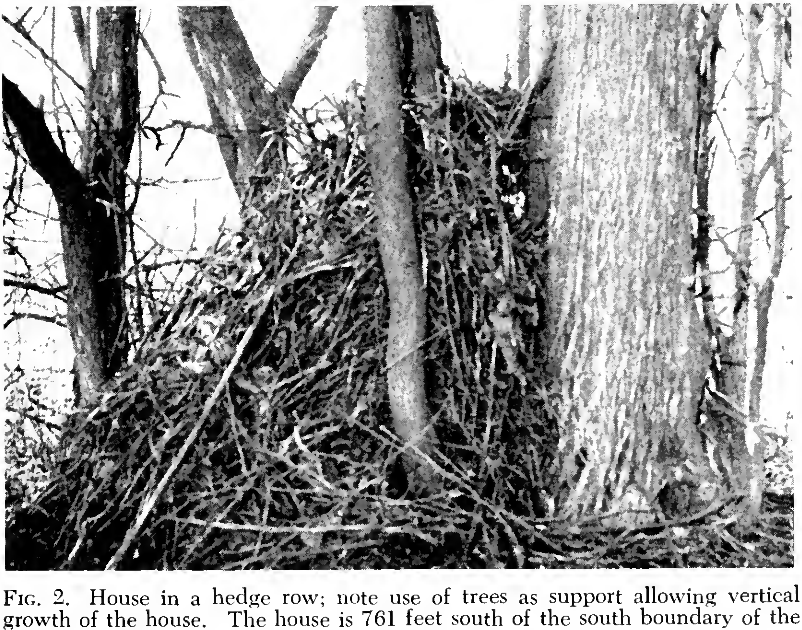
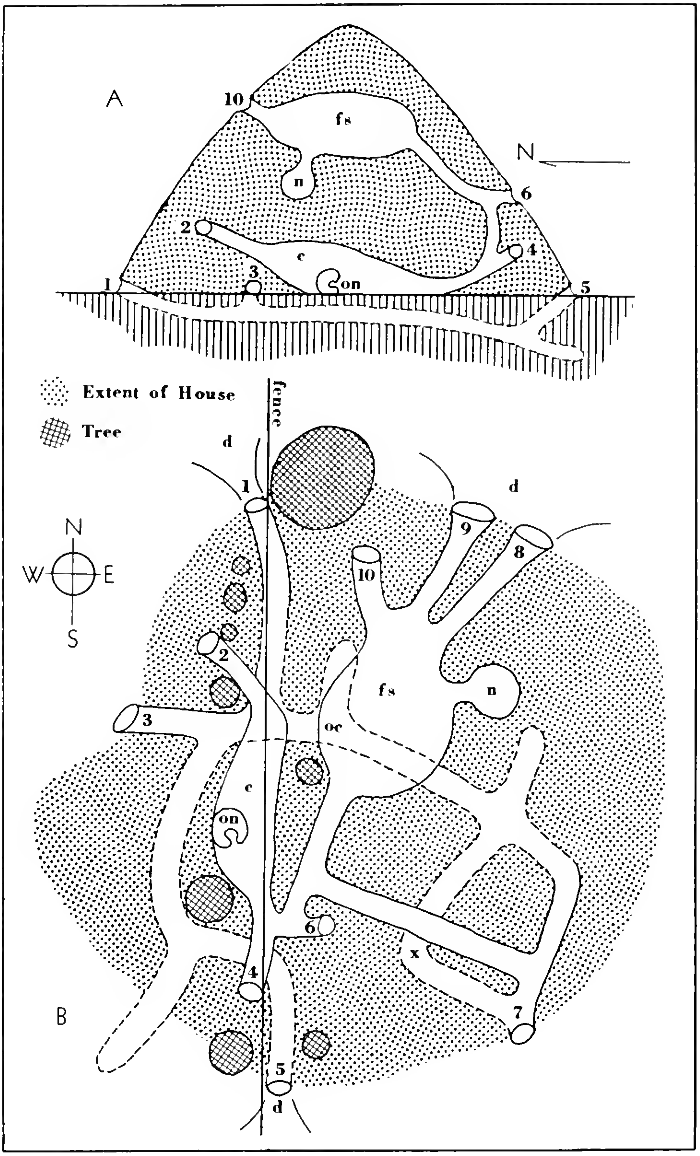


FIG. 2. House in a hedge row; note use of trees as support allowing vertical growth of the house. The house is 761 feet south of the south boundary of the Reservation. November 17, 1953.

Fig. 1. View of a part of the study area. The outcrop of rock extends along the horizon. July 27, 1954.

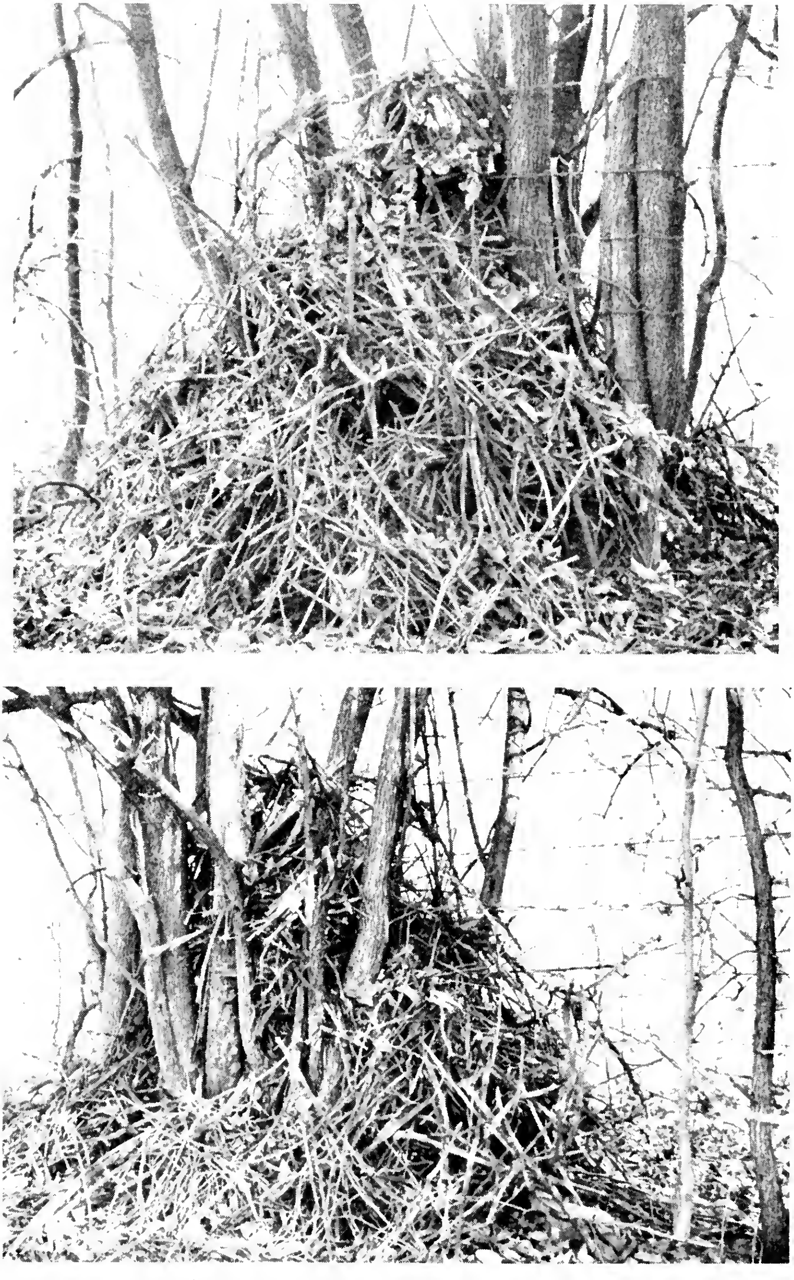
Fig. 2. West side of house shown diagrammatically in Plate 7. Southeast corner of Reservation on private land. November 17, 1953.

PLATE 7



(A) Diagrammatic side-view of a house typical for hedge rows. (B) Floor plan of the house drawn to the scale of one inch to eighteen inches. fs = food store; d = debris from inside the house; n = nest chamber; on = unused nest chamber; c = chamber; oc = osage orange cuttings; x = site of opened coffee beans and walnuts. See Fig. 2 of Plate 6, showing same house.

PLATE 8



Two views of one house from opposite sides of the hedge row illustrating use of both fence and trees for support. House was 921 feet south of the southeast corner of Reservation. November 15, 1953.

A woodrat house in a hedge row 15 mi. E Talmage, Dickinson County, Kansas, five feet from the ground. July 28, 1954.

PLATE 10

Fig. 1. A house at the edge of an old well three feet from the trees of a hedge row, 3 mi. S, 1 mi. W Hamilton, Greenwood County, Kansas. July 27, 1954.

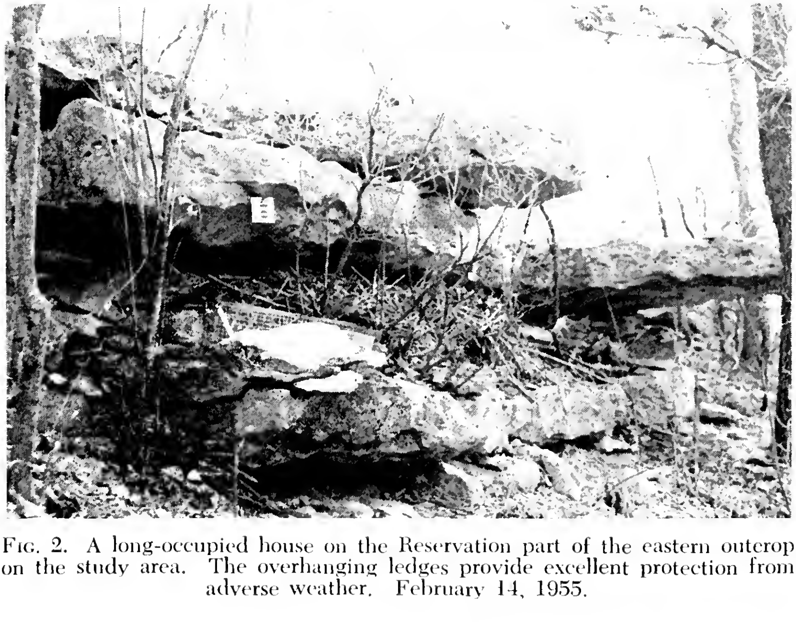


Fig. 2. A long-occupied house on the Reservation part of the eastern outcrop on the study area. The overhanging ledges provide excellent protection from adverse weather. February 14, 1955.

PLATE 11

Fig. 1. A house in the pastureland part of the study area and constructed of common ragweed stems. February 14, 1955.

Fig. 2. The low rock fence separated the woodland and pastureland parts of the study area. A house was at the base of the old elm snag. A tangle of wild grape vines covered most of the house. February 14, 1955.

Fig. 1. A woodrat house on a south-facing slope in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas. Note density of vegetation on slope. July 30, 1954.

Fig. 2. A well-built, cone-shaped house on a wooded slope in the Flint Hills, 7 mi. S Manhattan, Riley County, Kansas. Fragrant sumac in front of the house provided support and permitted such a shape. July 30, 1954.

protected also by the overhanging limbs while foraging on the ground.

Woodrats are seldom found in isolated or frequently trimmed hedge rows. They are most numerous where the rows are interconnected over large areas. An area investigated in Greenwood County in the summer of 1954, was found to include excellent habitat for woodrats (Fig. 2, Pl. 2); hedge rows were numerous and encompassed all sides of several sections of land. In most instances, however, only a part of each mile of row was suitable for houses. Three interconnecting rows, each one mile in length, were investigated for the presence of woodrats. In each case, approximately half of the row was suitable for houses although the remaining parts were dense enough to allow traveling. Thirteen houses were found in each of two rows and ten houses in the third; a total of 36 houses in one and one-half miles of rows. Judging from the sign around the houses, nearly all appeared to be occupied. In a similar area in the same county, eight occupied houses were found in another row approximately one-fourth mile in length. Since hedge rows were planted, the osage orange has spread so that now in many places this tree along with honey locust (or honey-shuck, *Gleditsia triacanthos* L.) forms woodland of considerable size where original trees have been cut or original prairie has been destroyed. Woodrats have been found in such woodland of osage orange and locust. Houses are built at the bases of trees or up in them.

Because rock outcrops furnish suitable cover both for houses and for foraging, requirements are more easily satisfied near rock outcrops than they are in hedge rows. Usually the houses are not so large in this situation as in the hedge rows.

Rock fences prepared in the process of clearing land for cultivation are frequently utilized by woodrats as house sites (Fig. 2, Pl. 3). Shrubby plants which commonly grow along these fences especially fragrant sumac (*Rhus aromatica* Ait.) furnish good support for the houses. Frequently, these fences are used as travelways.

Habitat in the Flint Hills is restricted. The vegetation is predominantly blue-stem grass (*Andropogon Gerardi*). Extensions of the forests of eastern Kansas are found along stream courses and on the valley slopes (Figs. 1, 2, Pl. 4). On the rocky slope north of a small stream seven miles south of Manhattan, Riley County, Kansas, in the summer of 1954, 11 houses found within a distance of approximately 100 yards were mostly low and spreading, not conical as are most houses in hedge rows. Some of the houses utilized rocks for support while others were constructed around the bases of fragrant sumacs. The trees were principally burr oak (*Quercus macrocarpa*) and chestnut oak (*Q. Muehlenbergii*). There were a few scattered honey-shucks (*G. triacanthos*) and American elms (*Ulmus americana*); the understory was composed of dogwood (*Cornus Drummondi*), redbud (*Cercis canadensis*), fragrant sumac (*R. aromatica*), and coralberry (*Symphoricarpos orbiculatus*). The south slope lacked the dense understory found on the north slope, and only two old unoccupied houses were found. Three occupied houses were found along an exposure of large limestone boulders at the crest of a small hill in another area of the Flint Hills (Fig. 3, Pl. 4). Dogwood formed a low dense thicket among the rocks. Woodrat houses were built on the boulders and utilized some of the dogwoods for vertical support. The surrounding area was entirely open grassland except for a few dogwoods on the hilltop.

Buildings such as barns, uninhabited houses, and storm cellars, are favorite haunts for woodrats. In some cases, sticks and trash are brought from the outside in great amounts and used to construct houses. Woodrats occasionally invade barns and garages that are in use. Their presence is easily detected and most generally, attempts are made to remove them. In some circumstances they gather and store large amounts of fruit or nuts considered valuable by the owner of the building.

Study Area

While certain aspects of the study, such as collecting specimens for laboratory use and dismantling houses, were carried out in other locales, live-trapping was confined to an area of approximately 58 acres in northeastern Douglas County. Nine acres of the study area were on the University of Kansas Natural History Reservation and the remainder on adjacent privately owned farmland. Nearly all the area was woodland (Fig. 1, Pl. 6). Douglas County is in east-central Kansas in the ecotone between eastern deciduous forest and western grassland.

Woodrats occurred locally in colonies where habitat conditions were optimum, and were most abundant along a limestone outcrop approximating the 1050-foot contour. This outcrop, an exposed edge of a stratum of Oread limestone underlying the shallow glacial till of the hilltops, constitutes a prominent physiographic feature of the Reservation and surrounding areas. Approximately 20 feet below the level of the hilltops is another stratum of limestone, but it is not exposed to the extent of the upper one. For purposes of convenience, no distinction is made between the upper and lower outcrops in following discussions. The upper outcrop varies in thickness from two to six feet. The face of the outcrop is deeply fissured, cracked, and has numerous ledges of overhanging rock. Boulders and smaller rocks broken from the outcrop are strewn down the hillside (Fitch, 1952:8).

Live-trapping was done along a 750-foot "eastern part" of a southwestern exposure of a limestone outcrop and along a 650-foot "western part" of the outcrop separated from the first by approximately one-fourth mile of woodland. Both were parts of the same outcrop, but the connecting stretch passed through an overgrazed pasture which was unsuitable woodrat habitat. The continuous eastern part was divided between three areas long under different ownership and subjected to land uses that had resulted in differences in vegetation: a 400-foot stretch on the Reservation, a 100-foot stretch in adjoining woodland, and a 250-foot stretch in open pastureland. The latter part was the only part of 1500 yards of outcrop in the overgrazed pastureland that was inhabited by woodrats. After extending through the pastured area, the outcrop where the western part was located again entered woodland. At the western part, approximately half the distance of the outcrop had an eastern exposure; the remainder had a southern exposure. A rock fence separating the woodland from the pastureland and connecting the eastern and western parts of the outcrop, was utilized to a certain extent for house sites and as a travel route.

Plants were counted on a series of quadrats taken along the eastern part in July, 1952, to determine differences in vegetation as reflected by varying land uses. The results are given in Table 1. The Reservation has been protected from grazing and cultivation since 1948, and along the outcrop and on the hillside below is an extremely dense thicket of dogwood, with also more kinds of smaller plants than on the remaining two portions of the eastern part. Important food plants rank higher in terms of abundance. A few hackberry trees (*Celtis occidentalis* L.) occur along the outcrop.

The woodland part of the study area was grazed by cattle. Trees were principally osage orange with scattered honey-shucks and elms. According to Mr. J. F. Morgan, a life-long resident, there were no trees here except for a few on the crest of the hill at the turn of the century. Coralberry began invading the hillsides by 1920 and osage orange had appeared in the late twenties. At present coralberry is the dominant small plant. Ground cover is not so dense along this part of the outcrop as along the part on the Reservation.

Plants indicative of overgrazing dominated the pastured area. These plants rank low in palatability to woodrats. Trampling of horses and swine had resulted in an almost complete disappearance of plants in the vicinity of the outcrop. This lack of ground cover coupled with lack of desirable food items probably accounts for the scarcity of woodrats along the part of the outcrop located in the pastureland.

Table 1. Differences in Vegetation, Reflecting Varying Land Usage, Along the Eastern Part of the Outcrop. Figures are Based on Counts from 75 Quadrats

Species	Percent of total count		
	Reservation part	Woodland part	Pastureland part
White Snakeroot (*Eupatorium rugosum*)	69.8	.5	absent
Dogwood (*Cornus Drummondi*)	7.6	11.2	.5
Bittersweet (*Celastrus scandens*)	5.7	absent	absent
Goldenrod (*Solidago* sp.)	5.4	3.3	absent
Hackberry (*Celtis occidentalis*)	2.3	17.4	3.4
Virginia Creeper (*Parthenocissus quinquefolia*)	2.1	.2	.3
Avens (*Geum canadense*)	1.5	2.4	absent
Fragrant Sumac (*Rhus aromatica*)	1.3	.2	absent
Sunshine Rose (*Rosa arkansana sulfata*)	1.3	absent	absent
Dropseed (*Muhlenbergia Schreberi*)	.8	absent	absent
Greenbriar (*Smilax tamnoides*)	.6	.4	absent
Smooth Sumac (*Rhus glabra*)	.5	1.8	absent
Winter Grape (*Vitus vulpina*)	.3	absent	absent
Leadplant (*Amorpha canescens*)	.2	absent	absent
Compass Plant (*Silphium laciniatum*)	.2	absent	absent
Poison Ivy (*Rhus radicans*)	.2	absent	absent
Coralberry (*Symphoricarpos orbiculatus*)	.2	59.2	4.6
Wild Licorice (*Galium circaezans*)	absent	2.5	absent
Bush Clover (*Lespedeza* sp.)	absent	.4	absent
Mullein (*Verbascum Thapsus*)	absent	.2	absent
Ironweed (*Vernonia Baldwini interior*)	absent	absent	44.2
Common Ragweed (*Ambrosia artemisiifolia elatior*)	absent	absent	33.1
Marijuana (*Cannabis sativa*)	absent	absent	11.0
Sunflower (*Helianthus annuus*)	absent	absent	2.2
Snow-On-The-Mountain (*Euphorbia marginata*)	absent	absent	.5
Black Nightshade (*Solanum nigrum*)	absent	absent	.2
Total count	609	552	644

Moisture Requirements

Observations on woodrats in captivity indicate that in nature the need for water, either free or from green plants, is important. The water content of fresh lettuce given regularly will satisfy the needs of captives, but foods deficient in moisture content must be supplemented by a supply of water. Woodrats deprived of water in summer dehydrate rapidly and lose weight. When free water is given to thirsty captives, they have frequently been observed to drink as much as five minutes without pausing.

In a 24-hour period, two captive rats having access to lettuce which had lost most of its water content consumed 28 and 22 cc. of water. The maximum temperature was 92° and the minimum was 73°. In the second 24-hour period, they consumed 34 and 36 cc.; maximum temperature was 93° and the minimum was 76°. The food was dry dog biscuits. In the third period with the same food, they consumed 64 and 58 cc. of water. The maximum temperature was 92° and the minimum was 73°.

In nature, water requirements are probably satisfied from dew, rainwater, and green plants. Much vegetation died in the drought summers of 1952 and 1953, and there were many consecutive nights without a trace of dew. Seemingly, it would have been difficult for woodrats to meet their water requirements. Moisture deficiency possibly was an important factor in the rapid decline of the population in the woodland section of the study area; however, individual records in 1952 are not complete enough to permit conclusions as to effects on their general health.

The mulch and soil beneath woodrat houses are normally moist even though soil is dry elsewhere. Houses dismantled in 1953 were extremely dry throughout, and the soil beneath them was dry to a depth of more than six inches. Throughout some houses there were heavy deposits of dust which may have been harmful to the occupants.

Owing to the better overhead cover, heavy amounts of rainfall probably do not handicap woodrats dwelling at outcrops as much as those living in stick houses in open woodland. Record amounts of rainfall in 1951 resulted in flooding but seemingly had little effect on adult woodrats; however, young may have been harmfully affected.

Relation to Heat

Within the protection of their houses, woodrats are well insulated and are able to withstand hot weather. Excessively high temperatures were common in the summer of 1954. Three females were kept in captivity in sheltered outdoor cages where a maximum-minimum thermometer registered temperatures as high as 112° F.; all survived. On several occasions, however, rats exposed to direct sunlight while in live-traps were found dead even though the air temperature was not excessively high. Others not dead were in a weakened condition and probably died after release because they were never caught again. Seemingly, after exposure to high temperatures they are not able to recover. The usual signs of heat prostration are wet fur around the mouth, rapid breathing, extreme lethargy, and inattentiveness to surroundings.

Houses constructed under overhanging ledges of outcrops are protected to a large degree from direct sunlight and the temperature is much more stable inside the house than outside both in summer and in winter. On August 29, 1953, an outdoor-indoor type thermometer was used to record temperatures every hour for 12 hours within a house constructed under an overhanging ledge, and at the same time, this thermometer recorded outside air temperature. Hourly readings, made from 7 A. M. to 7 P. M. inclusive, were as follows, figures in parenthesis representing air temperatures outside the house: 76, (79), 78 (79), 82 (82), 85 (88), 90 (92), 92 (95), 94 (99), 96 (101), 98 (106), 99 (106), 96 (103), 93 (94), 91 (92). Sunlight reached the house for a short interval in the day.

Maximum-minimum temperatures in consecutive 24-hour periods were also recorded for several houses along the outcrop in different seasons of the year. One maximum-minimum thermometer was inserted as far back under the ledge as possible among the sticks of the house and another one was set up in an outside shelter. Temperatures were recorded approximately the same time each morning. Table 2 gives the results recorded at one house in a warm period while Table 3 gives the results recorded at the same house in a cold period. In the hottest part of the day the temperature within the house remained 5 to 16 degrees cooler than outside air temperature; however, owing to the heat retaining qualities of the rock, minimum inside readings were somewhat higher than outside readings. In cold weather the latter situation is advantageous to woodrats.

Woodrats that remained in a live-trap throughout the night were able to maintain their body temperatures even though the air temperature was either cold or hot. Table 4 shows rectal temperatures taken in May and June, 1953, compared to air temperatures taken at the time the rat was removed from the trap.

Relation to Cold

Woodrats provided with adequate food and nesting material are able to withstand considerable cold when in live-traps, and have been known to pass the night without any ill effects at temperature as low as 22° F. On October 18, 1952, an adult male was caught in a live-trap that was not provided with either a nest box or nesting material. The temperature dropped to 30° F. during the night.

TABLE 2. COMPARATIVE MAXIMUM-MINIMUM 24-HOUR TEMPERATURE RECORDINGS INSIDE A WOODRAT HOUSE AND OUTSIDE THE HOUSE IN A PERIOD OF HOT WEATHER.

Date	Temperature recordings (F.)			
1953	Maximum readings		Minimum readings	
	Outside	Inside	Outside	Inside
September 6	85	80	62	67
September 7	91	81	63	65
September 8	88	76	62	66
September 9	92	84	68	69
September 10	97	90	70	72
September 11	100	94	67	72
September 12	102	86	56	64

TABLE 3. COMPARATIVE MAXIMUM-MINIMUM 24-HOUR TEMPERATURE RECORDINGS INSIDE A WOODRAT HOUSE (SAME HOUSE AS IN TABLE 2) AND OUTSIDE THE HOUSE IN A PERIOD OF COLD WEATHER.

Date	Temperature recordings (F.)			
1953	Maximum readings		Minimum readings	
	Outside	Inside	Outside	Inside
February 9	73	74	38	41
February 10	74	64	40	42
February 11	70	56	22	34
February 12	57	50	17	27
February 13	64	58	36	34
February 14	68	62	52	50
February 15	80	73	61	59
February 16	68	66	33	42
February 17	66	57	37	42
February 18	69	62	37	41
February 19	68	63	46	47

Table 4. A Comparison of the Body Temperatures, and Air Temperatures at the Trap Site, in Warm Weather and in Cold Weather of Several Live-trapped Rats.

Date	Sex	Body temperature (F.)	Air temperature (F.)
WARM WEATHER			
May 30, 1953	Female	103	101
June 3, 1953	Female	101	83
June 3, 1953	Female	97	83
June 4, 1953	Male	97	86
June 7, 1953	Female	101	88
June 7, 1953	Female	101	88
June 8, 1953	Male	99	77
June 9, 1953	Female	101	91
June 9, 1953	Female	104	96
June 10, 1953	Male	97	77
June 13, 1953	Male	101	80
June 14, 1953	Female	100	85
COLD WEATHER			
December 14, 1953	Male	95	26
December 14, 1953	Female	97	28
December 15, 1953	Female	97	28
December 15, 1953	Male	97	32
January 6, 1954	Male	95	34
January 6, 1954	Male	94	28
January 6, 1954	Female	98	28
January 7, 1954	Female	93	28
January 7, 1954	Male	95	28
January 8, 1954	Female	93	28
January 8, 1954	Female	95	49

The body temperature of the rat when taken after removal from the trap was 98° F. There was no apparent harm to the rat which survived in the area for five months thereafter. When provided with cotton nesting material, a rat in a live-trap would form a nest which almost entirely enclosed its body. In many instances when the temperature was low, the rats were observed to shiver much as humans do when they are chilled.

Probably woodrats are not harmed to the same extent as are some other small mammals by winter weather conditions such as prolonged accumulations of snow, chiefly because of the protective nature of their houses and the stored food supply. Extreme low temperatures when of short duration are not harmful. Rats in captivity have withstood temperatures as low as —7° F. without damage provided they had ample food and nesting material, but under certain conditions extremes of weather can cause heavy mortality.

Table 4 includes rectal temperatures compared with air temperatures in cold weather. It will be noted that body temperature tends to range slightly lower in cold weather.

Relation to Light

Woodrats are rarely seen in daylight. On a warm winter day a woodrat was reported seen at the site of an old quarry on the Reservation sunning itself on a rock. On another occasion, I observed one dust bathing approximately two feet from its house in a brush pile. The animal had sufficient protection but was in midafternoon sunshine. On June 2, 1953, at 3:15 P. M., a young woodrat (estimated to weigh 75 grams) was seen outside a house into which it escaped when I came into sight. When a woodrat is released from a live-trap, it usually pauses briefly, getting its bearings perhaps, and then it almost always runs to the nearest place that furnishes some shade. Ordinarily these rats exhibit an extreme dislike for bright sunlight. However, one that is hungry may venture to sunlight long enough to clip off a plant and take it to shelter to be eaten.

On dark rainy nights woodrats are usually more active than on clear nights. Seemingly, this is directly the result of increased darkness. However, the rats dislike getting wet, and forage in slack periods in the rain. In October, 1954, I had an opportunity to observe the behavior of a woodrat on a rainy night. An adult male lived in the garage on the Reservation and had constructed a nest behind some large pieces of fiber board. This nest was not covered by sticks and the animal could easily be observed at night with a red light. Even in the day it remained dark enough so that a light was necessary to see the rat. On the afternoon of October 21, 1954, a live-trap was placed in the garage. By 7:45 P. M. the rat was in the trap; he was marked and released whereupon he went directly to the nest. It was not yet totally dark. Soon rain began and by 10:30 P. M. the rat had not left the nest to forage. At 11:30 P. M. rain had stopped and the rat was not in the nest. The following night was clear. The rat was in the nest at 6:35 P. M. but one hour later he was gone, and had not returned by 9:00 P. M. when observations were halted. This indicated that even in darkness, woodrats dislike foraging in the open when it is raining.

HOUSES

General Character

Shape, size, and construction of woodrat houses vary according to the sites where they are located. In eastern Kansas, woodrat houses are constructed almost exclusively of sticks, but if sticks are lacking in the immediate vicinity, large weed stems may be substituted. Houses in some locations are relatively inconspicuous. Those bordering small creeks frequently resemble drift material. Woodrats sometimes actually incorporate and elaborate such a drift pile into a house. Volume of houses varies considerably and is related to location. Some consist of no more than a few sticks scattered over one end of a hollow log or around a rock crevice, and seem to serve no purpose, beyond the expression of the collecting instinct. Exceptionally large houses may be up to nine feet in diameter, and four to five feet high. Shape depends on location; if a vertical object is available for support the house will be cone-shaped, but in the absence of such support, the house is flattened and considerably broader at the base. Growth of the house is always chiefly vertical as long as support is present, but when this is lacking, the house broadens at the sides and base. This woodrat characteristically adorns the top of the house with such objects as rocks, dung, pieces of bark, broken glass, bones, or any other strange object which may be in the vicinity.

Uses

When any other suitable cover such as deep crevices, or burrows are lacking, the house is of definite survival value for a terrestrial mammal the size of a woodrat. The house is an environmental adaptation serving as a retreat where many activities can be carried on under sufficient protection from enemies or weather conditions. As long as a woodrat is at home it is relatively safe from natural enemies, but vulnerability increases greatly when it moves away from the home shelter. Houses also serve as a means of escaping certain types of enemies. As the woodrat is primarily nocturnal in habits, the house serves for a daytime retreat where the animal can sleep, eat, or clean itself. Houses are vitally important in increasing survival of the young especially when they are temporarily left alone. Abandoned houses are frequently utilized as temporary shelter for woodrats moving from one area to another thus increasing the likelihood of interpopulation flow which is important in colony stabilization. The house, if in good condition, furnishes protection from rain, snow, and excessive heat. Well-maintained houses can withstand considerable rain before becoming wet throughout. The instinct for storing food is highly developed in woodrats. The house is used as a storage place where green plant material will remain fresh for a considerable length of time; the food is partly protected from other animals which might pilfer it.

Signs of Occupancy

The general appearance of the house cannot always be relied on to ascertain whether or not it is occupied. In general, a house in a hedge row is peaked if occupied. Flattened houses in such situations are rarely inhabited although they may be used as temporary shelter. Many occupied houses that are low and flat have been observed in other situations. Recent droppings indicate occupation; they are usually in piles of varying sizes in one or two places just outside the house near the base or several feet away at a favorite site. Droppings less than 24 hours old are soft and almost black; those several days old turn progressively more brown, harden, and decrease in size as desiccation takes place. Debris or pieces of recently collected food at entrances usually indicate occupation. Under certain conditions, well-worn trails, void of leaves or other debris, leading from the house are good evidence that it is inhabited. In warm weather houses not in use usually have spider webs over the entrances although a period of time may elapse before this occurs. The appearance of sticks on the surface, whether recently collected or not, could not be used as a criterion of occupancy. There has been no evidence that sticks are collected by gnawing them from larger limbs or trees, but to the contrary, it is my impression that they are collected on the ground from fallen twigs or rotting limbs. Large weed stems are perhaps gnawed into smaller pieces but these are seldom used.

Structure

Most houses of woodrats in this area are basically similar although there are differences in degree of complexity and arrangement; houses along outcrops form an exception to this. Because of the intensive use of fissures and crevices, systems of tunnels are not developed. A nest chamber could not be found in either of two such houses which were dismantled. In a given area, houses in close proximity to one another will vary in extent of tunneling both above and below ground. Tunnels are often dug in the matrix of old droppings, rotted wood, and discarded food material which accumulates to depths of six inches or more beneath the house. This material may be compacted so that the entire layer resembles a thick sheet of cork. The location of the nest chamber varies from ground level to a level considerably higher. Frequently, the nest is beneath roots or in the hollow base of a tree incorporated into the house. Size of the nest chamber varies but little. Most nests are spherical and approximately six inches in diameter; however, the inner cavity varies according to size of the woodrat using it. The store of food is usually in one mass in the upper part of the house, but sometimes is divided into two or more parts. There also are one or more places where debris from inside the house is carried outside the house. Usually there are one or more places where the occupant habitually defecates; this may be just inside the house or several inches away.

Numerous houses were dismantled in order to study their structure. A large house located in the hedge row which grew on private land adjacent to the southeastern corner of the Reservation is here described as representative of those occurring away from rock outcrops in this area. A diagrammatic side view and floor plan of a house occupied by a subadult female is given on Plate 7.

This house also relied on support of both osage orange trees and a cattle fence (Fig. B, Pl. 7). Osage orange sticks were used mostly for building materials, but several ragweed stems were scattered over the surface. In the north-south direction, the house was 64 inches wide at ground level and 18 inches at the top. The house was 35 inches high.

There were ten well-defined entrance holes, six at ground level the others part way up on the sides. There were accumulations of old droppings and bits of osage orange fruit expelled from the house about entrances 1, 5, 8, and 9. A mound of soil free from debris, where the occupant probably took dust baths, was at entrance 3. Tunnels passed through the soil and a six-inch compacted layer of midden, droppings, and decomposed wood on which the house rested. The depth of this basal layer of midden indicated that the house was old.

The food store in this house, situated only a few inches below the top, measured 21 inches long and 16 inches high. The bulk of the stored food consisted of osage orange leaves, but a few pieces of the fruit were also found. There was a small amount of old leaves collected the previous season. A platform in a small chamber formed by the convergence of three tunnels at the north end of the food store had an accumulation of droppings, empty osage orange seeds, and leaf fragments. Indications were that most of the feeding was done on this platform. The occupant had been removing food from this end of the cache only.

The nest was below the food store but not at ground level, and sticks of the house supported it. It was globular, six inches long and five and one-half inches wide; the inner cavity was four inches deep and three inches wide. The nest was made from shredded bark and smaller amounts of grass blades.

Entrance 2 was 17 inches from the ground up on the side of the house, and led to an enlarged chamber at ground level which measured 19 inches long and six inches high. Entrances 4 and a branch from 6 extended down to the south end of this chamber. Old droppings formed the floor of the chamber. A few pieces of osage orange fruit with the seeds removed and an old misshapen nest were found within the chamber. Entrances 1, 3, and 5, led to subsurface tunnels. The debris about 1 and 5 probably resulted from the excavation and enlargement of these tunnels. The bases of the hedge trees were undermined by these subsurface tunnels.

Tunnels leading from entrances 1 and 3 joined to form a system which emerged at entrance 7. At the place where a short blind tunnel branched off the main tunnel, several new cuttings of young osage orange twigs averaging three inches in length were found. A small rock, four ventral scutes from the shed skin of a snake, and a piece of a scat of an opossum, were near the cuttings. The tunnel passed almost straight beneath the house and near the east side branched into three tunnels, one ending blindly, and the other two again joining at entrance 7. In one of these branches several opened coffee beans, three opened walnuts, and two grains of corn were found. There were no conspicuous trails leading from this house; seemingly the occupant utilized the branches and trunks of the fallen trees for traveling.

Three additional houses located in this hedge row were studied. One had only three entrances and there were no distinct trails leading from the house (Fig. 1, Pl. 5); however, there was an extensive system of subsurface tunnels. The food cache was again near the top and the nest chamber was a few inches below. The nest rested on a platform of droppings and food debris; a short tunnel led to the food store.

Well-defined trails several feet in length ran along the hedge row from either end of another house. This house had seven entrances. Narrow strips of bark up to 31 inches in length had been pulled from a dying tree and placed on the sides of this house (Fig. 2, Pl. 5).

The third house also had only three entrances and the tunnel system was simple (Plate 8). Two of the entrances were connected by a runway and a branch of this led to the nest. Because the nest was immediately below the food store and at one end, a runway was not necessary to connect the two. The nest was five inches across and four inches deep on the outside; the entrance measured two and one-half by two inches and the cavity three inches deep. The small size of the subadult female (214 grams) occupying this house accounts for the small size of the entrance to the nest. The tunnel leading from the third entrance was so ill-defined that it could not be followed. One notable difference observed at this house was that the only fecal depository was deep within the house.

A large, excellently constructed house dismantled on January 31, 1953, demonstrated preference for a brush-pile site over a hedgerow site. Four small osage orange trees about 15 feet in height at one end of a hedge row had been uprooted in the construction of a cattle fence. Each of the trees had more than one trunk, and together they formed a dense tangle. The house, approximately eight feet from a country road, was in the midst of this tangle. It would have been almost impossible for any predator, except perhaps a snake, to capture the woodrat living in this house while the rat remained within the brush pile. There was overhead protection for approximately 10 feet in each direction from the house, and along the route to the nearby hedge row. The hedge row extending parallel to the country road did not have any houses in it. This house, one of the largest observed, was 56 inches high and 66 inches at its widest diameter; it was irregular in outline but pointed at the top. The trunks of the trees furnished support for the base while the branches supported the sides and permitted vertical growth.

There were several unusual features in this house. It had only two entrances at ground level, one on either side. One nest was a foot below the top, a second was two and one-half feet below the first, and a third was at ground level. The first nest was above the food store and in no other instance was this arrangement observed. Seemingly, the second nest was the one in use at the time the house was dismantled although the first still retained the characteristic shape. Perhaps the occupant occasionally used the first. The second nest had quantities of rabbit fur interwoven with the shredded bark and dried grass. The third nest, located at ground level, was obviously not in use. The food store was unusual in that it contained many osage orange twigs, eight to ten inches in length, with their leaves still attached. Usually only leaves removed from twigs are brought in. In addition, there were numerous droppings scattered throughout the food store and in no other instance was such scattering observed. From observations on other houses, indications were that the woodrat removed seeds from osage orange fruit only as needed in the course of eating them, but in this house, a small store of uneaten seeds was found.

A medium-sized house dismantled on December 2, 1950, had three distinct trails leading from it. The house was on a hillside and was built around the bases of two honey-shuck trees 12 inches apart, having a low fence nailed to them. A low rock fence ran along the row of trees, but it was almost covered by leaf litter and soil washed down the hillside. These trees acted as a prop because the terrain sloped sharply at the place where they grew. For this reason, most of the house was located on the uphill side of the trees. On the uphill side, the house was 19 inches from the ground to the top, but it was 37 inches high on the downhill side. Two trails approximately four feet apart ran parallel to each other on either side of the row of trees. They could easily be followed for approximately 20 feet, but they were indistinct beyond this. The third trail coursed in the opposite direction from the others and led directly to an underground burrow among rocks. This house had three separate stores of food, each with the same kind of food. The nest chamber was in the hollow base of one of the honey-shuck trees. The entrance was three inches wide and the interior, like all others observed, had no debris or droppings within. The day following that on which the dismantling was done, the site was revisited and it was found that the woodrat, which had not been captured, had placed a few sticks and a rock over the cavity in the tree where the nest formerly was located. However, a return trip six days later revealed no further attempt at rebuilding the house. This was the only record of an attempt to rebuild a dismantled house. In most cases, if the rat does not find shelter soon, it probably falls prey to an enemy.

Objects Found in Houses

The woodrat's peculiar habit of bringing to the house any object which it is capable of carrying is well known. Woodrats in captivity immediately respond with curiosity to any inanimate object placed in the cage. Such an object is soon moved to a chosen site in a corner or on top of the nesting material. Rocks, dung, and bones are the most common items found within houses. If an animal is killed or dies near a woodrat house, some of its bones will almost certainly be collected by the woodrat. Bones of opossums are found in houses especially frequently suggesting that often they die inside the house while using it as a refuge. Deposition of small rocks or dung on top of a house seems to represent a final stage in a period of work on the house. In many instances, an additional collection of rocks or dung can be found several inches below the surface which seemingly indicates the height of the house before the last period of repair. Numerous objects such as broken glass, cans, empty shotgun shells, and bits of paper, are commonly found in houses.

Houses in Hedge Rows

Houses built in hedge rows are usually well adapted to their immediate environment. The hedge rows provide all the necessary constituents such as cover, support, building material, food, and escape routes for supporting populations of woodrats. Hedge rows rank above all other types of house sites as far as type of support is concerned. Most of the better built and elaborate houses are found in hedge rows. Houses are permitted to undergo more vertical growth owing to the nature of support and considerably more protection from adverse weather results. Most of the houses are constructed at ground level but occasionally one is built up in a tree (Plate 9). An unused house in Greenwood County, Kansas, was built on loose boards at the edge of an old well four feet from the hedge row (Fig. 1, Pl. 10). This house was low and spreading, seemingly ineffective for protection.

In a hedge row typical of those that support woodrat colonies, 76 rods long, extending south from the south boundary of the Reservation, on a privately owned farm, there were 12 houses, all well-made and substantial, except one.

Land on the west side of the row was cultivated while that on the east side was not. After the wheat crop was harvested on the west side, there was almost no ground cover left away from the row. Coralberry grew beneath the osage orange trees of the hedge row. Ground cover on the east side was much more abundant both under the trees and away from them. It was perhaps for this reason that the bulk of each of the houses was on the east side. A wire cattle-fence 30 inches high was nailed to trees in the row. Two strands of barbed wire had been placed above the wire fence. The top strand was approximately 40 inches from the ground. This fence aided in supporting the houses.

Presence of small stumps indicated former trimming probably to increase density of growth, but the trees had long been untrimmed and were near maximum size. The limbs arched outward and many touched the ground 10 to 12 feet from the base of the tree. In summer, it was difficult even to see a house through the dense foliage; limbs had to be cut away in order to reach a house. The dense canopy furnished excellent shelter for the houses. Coralberry added to the density of the surrounding vegetation. The tough and thorny branches provided an effective barrier in keeping cattle from grazing near the bases of the trees.

Houses at Rock Outcrops

Houses at outcrops differ in form, in structure, and sometimes in size, from those in woodland or hedge rows. Some houses are large and others consist of no more than a few sticks piled against a crevice. Even some of the larger structures do not serve precisely the same function as a house in a hedge row. Food may be stored among the sticks but an elaborate tunnel system is lacking; crevices and burrows among the rocks are used instead. The collection of sticks does serve an important purpose in preventing entrance of enemies and providing protection against adverse weather. Houses at outcrops are almost always more effectively protected from heavy rain, snow, or direct sunlight than houses elsewhere. Moreover, when trips are made away from home for feeding or breeding, an outcrop is an excellent route for traveling, with overhead protection and access to the fissures in the outcrop or spaces under boulders in the event that an enemy is encountered. Outcrops are also good avenues for woodrats migrating in search of new homes. Woodrats have tended to survive better when living at the outcrop than elsewhere. Catches were made in live-traps more consistently on the study area at the outcrop than in the woodland. In July and August, 1952, disturbance of traps at the woodland houses was occurring almost every night until by late August woodrats could no longer be trapped and most of the houses were abandoned. Whether or not they were being killed and removed from the traps by predators could not be determined, as there was never any blood, fur, or other sign on or about the traps. In this period, woodrats were being caught at the outcrop fairly consistently but in small numbers.

Traps were kept at six houses along the eastern section of outcrop for the entire period of study. Initially, more traps were used, but when they consistently failed to yield captures, they were moved to other locations. Three of the houses were on the Reservation part of the outcrop, two on the wooded part, and one on the pastureland part. Live-trapping was not done at the latter house as much as it was at the others.

A large, favorably situated house on the Reservation typical of many of those along the outcrop, had sticks almost filling the space between overhanging rock and the layer at ground level (Fig. 2, Pl. 10). The house was 85 inches long, 36 inches wide, and 19 inches high with a southwestern exposure. The part of the outcrop forming overhead cover consisted of two thick layers, the uppermost one extending 19 inches beyond the second at one place. This top layer extended 94 inches from the soil and was 10 inches in thickness. The distance from the outermost edge of this layer to the ground was 62 inches. The overhanging shelf sheltered the mid-portion of the house which tended to follow the contour of the second upper layer. The second layer was 11 inches thick midway over the house. The layer of rock upon which the house rested was 10 inches in thickness. Between it and the ground, there were numerous holes and fissures. In summer this house was in direct sunlight only in mid-morning and late afternoon. In winter it was protected from wind and blowing snow from the north. The dense thicket of dogwood which grew down the hillside in front of the outcrop furnished some protection from the south. A prairie field lay back of the outcrop. Dominant vegetation in order of estimated abundance was: white snakeroot, dogwood, fragrant sumac, plum (*Prunus americana* Marsh.), wild grape, hackberry, smooth sumac, and bittersweet. Ground in front of the outcrop and in the dogwood thicket was almost a solid carpet of white snakeroot. However, small dogwood and hackberry seedlings were numerous. A group of fragrant sumacs supported the west end of the house; two small dogwoods supported the east end. There were 17 small to medium-sized hackberry trees within 50 feet of the house. Grape and bittersweet grew back of the outcrop at the margin of the prairie field. Availability of excellent shelter and abundant preferred food caused this house to be occupied almost continually throughout the period of study, and a total of 16 woodrats were live-trapped there, including permanent occupants, nightly visitors, and others that stayed temporarily, especially when the population became low and there were other nearby empty houses. Throughout the period of study, the house gradually deteriorated but not to the extent that some of the woodland houses did. The most noticeable change was reduction in height of the pile of sticks which increased the size of the space between the top of the house and the overhead ledge of rock. When the house was at maximum development, sticks filled the space between the upper and lower ledges of rock; however, for much of the time it remained in the condition shown in the photograph. Woodrats released after capture frequently ran directly under the upper ledge and sat on top of the house for several minutes cleaning their pelage. Others would disappear under the layer of rock at ground level. Crevices probably connected with the interior of the house.

At the same outcrop approximately 175 feet from the house discussed above, was another house also favorably situated with respect to shelter and food supply, and similar in dimensions; 84 inches long and 19 inches high. It was protected by a large overhanging ledge and many loose stones in front of the house provided escape routes. A dense thicket of grape and bittersweet grew at the edge of the outcrop above the house. A total of 15 different rats were caught in live-traps at this house.

A second type of situation for houses at the outcrop was under large slabs of rock broken away from the exposure. A live-trap was kept at a house in such a situation throughout the study period. The site was on the woodland part of the eastern section. This house was not so large as the two previously described but was maintained equally well. A total of 18 woodrats were live-trapped at this house.

When the population was reduced to a few rats in 1953, house repair was neglected in all the houses along the outcrop. The few remaining individuals tended to roam from one house to another rather than settling permanently in one house. Seemingly, repairs are made only by permanent inhabitants. Therefore, stability of numbers is important in maintenance of houses. To remain in good condition, a house needs to be permanently occupied at all times. The population is a healthy one if all houses are filled and there is competition for these houses.

Houses along the part of the outcrop in the overgrazed pastureland were made from dead ragweed and sunflower stems owing to lack of sticks. Houses constructed of this type of material are flimsy and cannot offer as much protection to the occupant as stick houses. Woodrats building such houses probably are able to survive because of the crevices and underground burrows (Fig. 1, Pl. 11). Perhaps if overcrowding of more suitable parts of the outcrop occurred, this part would be used more. Houses at the western section of outcrop were constructed in similar sites and were similar in form to those at the eastern section.

Houses in Rock Fences

As previously mentioned, man-made rock fences are frequently used as sites for construction of houses. Innumerable holes and crevices among the rocks provide means of escape from enemies. There are many sites available for temporary daytime retreats for migrating rats.

Two houses on the study area were located along a rock fence separating the woodland area from the pastureland. One house was made within a clump of fragrant sumac. The rock fence supported the back of the house while the sides and front were braced by the sumacs. The plants, when leafed out in summer, shaded the house for most of the day. This house was inhabited by a female rat from October, 1951, to March, 1952. After she disappeared the house was never again occupied. A second house, approximately 100 feet from this one, at the base of an old dead elm (Fig. 2, Pl. 11), was large and low. Wild grape almost completely covered the snag in summer and furnished excellent cover for the house. The rock fence and base of the snag furnished support for the back of the house. Fallen pieces of the old tree and some of the grape vines supported the sides. Seemingly, this house was used chiefly as a temporary refuge by woodrats migrating along the fence. One adult male occupied it approximately three months, but after he disappeared it was never again permanently inhabited. Another adult male caught once at this house appeared almost a month later at the outcrop and settled permanently at a house there. Principal food items in the vicinity of the two houses at the rock fence were: osage orange, dogwood, and honey-shuck. Live-stock habitually used trails on either side of the fence. This may have been a factor in discouraging construction of additional houses. Neither of the two houses were on the pastureland side of the fence perhaps as a result of the rooting of swine present there. A house was observed at a rock fence in another area built around several small box-elders (*Acer Negundo* L) growing up through the fence.

Houses in Woodland

One of the populations of woodrats on the study area occupied houses constructed in piles of brush left after small scale clearing operations (Fig. 2). Sticks in the brush heaps piled two years before and some four years before according to the owner, interviewed in July, 1952, were mainly osage orange with smaller amounts of dogwood. The area was wooded chiefly with osage orange, honey-shuck, red elm, and dogwood. Cattle grazed on the area and weedy species such as ironweed and snow-on-the-mountain were abundant. Smooth sumac, fragrant sumac, and coralberry were common. Live-trapping operations were started here on March 29, 1952, and continued intermittently until June 20, 1954. However, most of the trapping was done in April, May, June, and August of 1952 and June and August of 1953. In early 1954, the owner burned most of the houses and in June, 1954, the remaining houses were abandoned. When investigated in February, 1955, they were still empty and rapidly deteriorating.

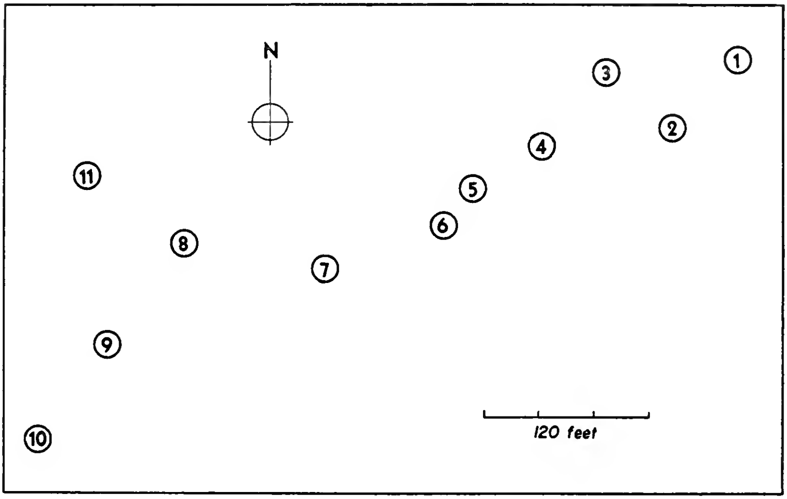


FIG. 2. Diagram of the eleven woodrat houses in the woodland part of the study area. Each of the houses, except house 11, was in a brush pile.

There were eleven piles of brush and in each of ten of them a woodrat house was constructed; an eleventh house was at the base of an osage orange tree. Except along the nearby rock outcrop, only five additional houses (two of them unoccupied, and one built in a brush pile) were found in the entire woodland part of the study area, demonstrating strong preference for brush pile situations. The size of the population under consideration seemed to be limited by the number of brush piles as there was no sign of construction of new houses throughout the period of study. Preference for brush piles as sites for houses probably results in better support and overhead protection for them. Dense tangles of limbs also provided additional protection from larger predators attempting to gain entrance into the houses.

The houses varied both in size and in external appearance. Some were large peaked structures whereas others were low and spreading; all were made from osage orange limbs.

House 9, a typical example, was both high and wide and possibly was the best constructed of all. Its south side faced a large open area in woods and the north side faced woodland. Surrounding vegetation included ironweed, dogwood, smooth sumac, osage orange, and one large honey-shuck tree. One limb of the honey-shuck tree offered some protection. From mid-afternoon until sundown, osage orange trees protected the house from sunlight, but the house was unshaded at mid-day. The height of the house probably compensated for lack of cover in mid-day, and, being of peaked shape, it tended to shed rain. Two smooth sumacs approximately five feet high supported the south side of the house and allowed vertical growth higher than the brush pile. Limbs of the brush pile extended away from the house in four directions for approximately 10 feet. Trails leaving the house utilized these limbs for overhead protection as far as possible. Several weed stems had been used as building material, but osage orange sticks were far more abundant.

Miscellaneous Sites

Houses of woodrats constructed inside buildings vary in size according to availability of materials. Sometimes, a woodrat is able to employ materials already present such as accumulations of boards or trash and little or no outside material is brought in. In one abandoned building a large accumulation of osage orange leaves was deposited on boards across rafters and the customary pile of sticks was absent. The nest chamber was somewhere between the walls. In other instances, large quantities of sticks are brought from the outside to construct a more typical house.

In the Flint Hills where there are steep shrubby slopes rising from small creeks, houses tend to spread downhill. A large rock or plant braces the lower end of the house and growth in height occurs at this place. One house (Fig. 1, Pl. 12) in such a situation was 110 inches long, 50 inches high at the lower end, 18 inches high at the upper end, and 74 inches wide. A few small fragrant sumacs and a limb on the ground braced the lower end. This was not completely adequate because the base was spreading somewhat downhill beyond the support. The house was approximately as high as possible and volume could increase only by spreading from the base. Another house on a comparatively level place several yards away was more typical in appearance (Fig. 2, Pl. 12). A small fragrant sumac braced the downhill side and small dogwoods supported the back. There were several houses on this slope (see pages 551 and 552); all were in an excellent state of repair. There were thickets principally of fragrant sumac, dogwood, redbud, elm, burr oak, chestnut oak, and honey-shuck. The opposing north-facing slope was not so steep and lacked the dense vegetation which resulted in preference for the south-facing slope.

Houses built along rimrock in the Flint Hills differed in appearance from those along outcrop farther east. The rimrock consisted mainly of loosely arranged boulders of varying sizes. There were no ledges and deep crevices. In one place investigated (see p. 552 and Fig. 3, Pl. 4), a rather dense but narrow thicket of dogwood grew among the rocks and the woodrats had used both plants and rocks as support for their houses. Sticks were piled between rocks at their bases, or around clumps of dogwood. Open grassland away from the rocks probably restricted woodrats to foraging only under the protective cover of the dogwood thicket.

Occupancy of Houses

Houses in favorable locations were usually occupied and visited by a succession of woodrats. The more favorable houses had histories of more continuous occupation. Occupation of houses usually reflects to some degree the condition of the population. When the population is high, a house made empty by disappearance of its owner will be reoccupied almost at once. On the other hand if numbers of woodrats are low, occupation may be slow.

The history of occupation is better known for several houses at the eastern section of outcrop than for those on the other two areas. The reason for this is that traps were kept at these houses throughout the study. The history of three of these will be presented as examples of succession of occupancy. Population trends are also reflected in these histories.

(1.) This house was occupied by an adult female in March, 1951. In May, an adult male took over and the female was forced to find another house. The male stayed until July. The house remained unoccupied through August but was inhabited by another adult male in September, and he remained until his disappearance in January, 1952. The population was low at this time and the house remained empty through February. In March, another adult male took possession and one subadult female visited the male. No live-trapping was done there in April, May, and June, 1952. In July, a new adult male was living in the house and he remained there until late November. Two nights of trapping in December did not result in a capture at this house, and seemingly it was empty through February and March, 1953. In May, an adult male was caught once but never seen again. The population by this time was extremely low and the few remaining rats, both males and females, were moving from house to house. It became almost impossible to establish ownership of houses. An adult male was caught here one time in June, but seemingly a subadult female "owned" it and was alternating between this one and another nearby house from June until she disappeared in mid-August. When trapping was resumed on September 6, an adult male had occupied the house and was still present on November 7. However, he moved and the house remained empty in December and January, 1954. Trapping was not resumed at this site until June, 1954, and a subadult male was then living there. It is of interest to note that this house was most commonly inhabited by males.

(2.) An adult female was living in this house in March, 1951. She maintained occupancy until her last capture on July 7, 1951. An adult male visited her in April and again in May. A juvenal female, presumably the offspring of the adult female, was caught in June. The young female disappeared in early July. No trapping was done in August, and in September, a juvenal male was caught there just once. In October, the house was occupied by another young male from another part of the outcrop. He remained until early December and was replaced by a larger male. The latter male disappeared in January, 1952. The house was not occupied in February and March. When trapping was resumed in July, a subadult female was living in the house and she remained until late November. She was visited by an adult male in July. The house was empty in December, 1952. In February, 1953, a subadult female was caught once but was never seen again. After this, the house seemingly was not permanently occupied although several rats were caught at this site. However, none of them was repeatedly recaptured. An adult male was live-trapped one time in each of the months of May, June, and September. Also in September, another adult male, and two subadult females, were live-trapped at this house; the male was again captured in November.

(3.) A subadult male was caught just once here on March 31, 1951, but he was never seen again. In April, the house was taken over by an adult female and she remained until the last capture on October 21, 1951. An adult male visitor was captured twice in April and three times in May. A subadult male visitor was captured here once in December, a different subadult male in February, 1952, and a young adult female in March. When trapping was resumed again in July an adult female that had been living at a nearby house was caught one time. Two juveniles, a male and a female, were caught here in July. Possibly the adult female had been living here previous to July, and after the young were weaned, she moved to the nearby house. Both young disappeared by the end of July. On September 8, a subadult female was found in a live-trap at this house but she disappeared and two days later a young male took possession and remained until November 22. He was seemingly forced out or captured by an enemy because a subadult female was caught on November 23. She was still living in the house in December. An adult male was captured once in November and once in December. The female seemingly stayed through January, February, March, and April. In May, a young female, probably the offspring of the female mentioned above was caught. She moved the first of June and the mother was again captured here in August. During the last half of 1953, the house was not permanently occupied by one individual. A subadult female was trapped here once in November and again in December. An adult male was captured once in December. The house was empty in January, 1954, and when trapping was resumed again in June, 1954, a subadult male was taken. The house was dismantled in February, 1955, and found to be unoccupied.

FOOD HABITS

Food items studied were mostly those found inside dismantled houses. Woodrats released from live-traps were observed on several occasions to eat certain plants. Their natural diet is composed largely of plant material although flesh, both cooked and uncooked has been eaten by rats in captivity.

Food habits of this species have not been studied in any detail. In Florida, Pearson (1952:460) fed several native plants to captive *N. f. floridana* noting acceptance or refusal of each. These captive animals had access to a constant supply of corn and sunflower seeds; therefore Pearson's results may not reflect the preferences of the animal under natural condition. In Alabama, Howell (1921:52-53) found that *N. f. floridana* was eating hickory nuts and papaw seeds.

Bailey (1905:110) found that *N. f. attwateri* in Texas was eating nuts and leaves of the walnut tree, cactus capsules and stems, acorns, juniper berries, wild grapes, blackhaw, mushrooms, and Mexican buckeyes. Also in Texas, Strecker (1929:220) found that woodrats ate pecans in great numbers.

This species of woodrat demonstrates great adaptability in its feeding habits and ability to thrive on almost any kind of plant material that is available. The type of food therefore is usually not a limiting factor. Quantity is basically more important than kinds. If a house is suitably located, the woodrat is able to subsist on most any kind of plant material in the vicinity as long as it is present in sufficient quantity for storage purposes.

The drive that compels woodrats to store food in quantity usually does not commence until in September or October. In 1951, the first sign that storing had begun was noted at a house occupied by an adult female on September 22. She had collected numerous dogwood leaves and six honey-shuck "beans". On October 7, 1951, a large number of white snake-root leaves, some loose and some attached to stems, had been brought to another house occupied by a young male. Both of the houses were at the outcrop. In each case the leaves were green but were becoming brittle. In 1952, signs of active food gathering were first noted on October 17. An adult male living in a house at the outcrop had brought in dogwood twigs, goldenrod plants, part of a compass-plant, and several bittersweet fruit, none of which had been noted one week previously.

Woodrats in this area do not store much food in spring and summer. Several occupied houses opened in July, 1952, were found to have little food within. One had a few osage orange and ironweed leaves; another had only a few osage orange leaves; two were completely empty; and the fourth had one ironweed plant and part of an old ear of corn.

Woodrats will often store more food than they can consume in winter and a substantial amount will be left when storing begins anew. On April 7, 1951, several empty bittersweet capsules were noted to have been carried to the outside from two houses at the outcrop. As bittersweet does not begin to flower until May, this must have been food stored the previous autumn. Several houses dismantled in early winter contained small quantities of osage orange leaves remaining from stores of the previous year. Leaves stored in autumn will remain green until the following spring but not until the following autumn. Seemingly, if the food store is depleted in winter, food will be collected and stored in early spring.

A house dismantled on June 12, 1952, contained a cache of fresh dogwood leaves. Several opened honey-shuck "beans" were found but no other usable food. The appearance of the dogwood leaves indicated they had been recently collected probably from a small dogwood plant growing up through one side of the house. In summer, woodrats probably do most of their feeding while foraging but frequently bring small amounts to the house for daytime feeding.

The urge to store food dominates all other activities once the drive has begun. Observations on captive woodrats indicate that in nature they would be highly vulnerable to predation during this period. Specimens kept in outdoor cages were regularly fed sunflower seeds placed in a small metal cup wired to the cage. In summer they were content to feed directly from the cups. However, a rather rapid change in behavior occurred with the advent of autumn. The seeds were removed from the cups by the woodrats and placed in a pile in one corner of the cage. Owing to the fact that the cages were provided with wire bottoms many of the seeds fell through to the ground. One female persisted in losing almost all of her food this way at each feeding. The seeds were at first removed from the cups only after the observer had left the vicinity of the cages, but soon the rats commenced removing them even before filling the cup was completed. The rats seemed oblivious to the presence of the observer. The food finally had to be changed to commercial dog biscuits large enough so that they would not fall through the bottoms of the cages. From these observations on animals born and reared in captivity, it seems that storing behavior is instinctive and not learned.

For the kinds of plants eaten in eastern Kansas see Table 5. Leaves and seeds of the osage orange tree comprised the bulk of the food store more often than all of the other foods combined. This is because the osage orange is abundant in hedge rows and woodland, and is highly preferred as a house site. Probably cover is a more critical factor than food in determining the choice of osage orange as a house site. Danger to the foraging rats from enemies is considerably reduced because the distance that the rat is required to go for food is only a few feet from the house or from a suitable escape route. The osage orange tree is extremely hardy and considerably more resistant to drouth than most other species of plants of this area. Osage orange trees produce prodigious crops of fruit; each fruit contains hundred of seeds. After falling, the fruits are slow to deteriorate but turn brown upon freezing. Of the vertebrate species living in this area, only the woodrat and squirrel use the fruit as food to any great extent, however, abundance overcomes any possibility of serious interspecific competition.

Both entire fruits and pieces are carried to the house. The fleshy seed coat usually is removed to the outside of the house and is discarded; only the seed is eaten. In every instance observed the stored fruit was accompanied by an equally large amount of leaves.

TABLE 5. PARTS OF THE PLANT FOODS WHICH WERE UTILIZED AND THE PLACE WHERE EACH OBSERVATION WAS RECORDED. OFTEN WOODRATS SEEK FOOD IMMEDIATELY AFTER RELEASE FROM A LIVE-TRAP; NUMEROUS OBSERVATIONS WERE RECORDED IN THIS MANNER.

Plants	Parts eaten				Where recorded	
	Leaf	Fruit	Seed	Stem	Food store	Sight record
Common Ragweed (*Ambrosia artemisiifolia*)	X	....	....	....	....	X
Bittersweet (*Celastrus scandens*)	X	X	X	....	X	....
Hackberry (*Celtis occidentalis*)	X	X	X	....	X	X
Lamb's-quarters (*Chenopodium album*)	X	....	....	X	X	....
Thistle (*Cirsium undulatum*)	X	....	....	....	X	....
Dogwood (*Cornus Drummondi*)	X	X	X	....	X	X
Red Haw (*Crataegus mollis*)	....	X	....	....	X	....
Honey-Shuck (*Gleditsia triacanthos*)	X	....	X	....	X	....
Coffee Tree (*Gymnocladus dioica*)	....	....	X	....	X	....
Black Walnut (*Juglans nigra*)	....	....	X	....	X	....
Osage Orange Tree (*Maclura pomifera*)	X	....	X	....	X	....
Climbing False Buckwheat (*Polygonum scandens*)	X	....	....	....	X	....
Wild Plum (*Prunus americana*)	....	X	X	....	X	....
Burr Oak (*Quercus macrocarpa*)	....	....	X	....	X	....
Chestnut Oak (*Q. Muehlenbergii*)	....	....	X	....	X	....
Fragrant Sumac (*Rhus aromatica*)	X	....	....	....	....	X
Smooth Sumac (*Rhus glabra*)	X	....	X	....	X	....
Poison Ivy (*Rhus radicans*)	X	....	X	....	....	X
Poison Oak (*Rhus Toxicodendron*)	....	X	....	....	X	....
Gooseberry (*Ribes missouriense*)	....	X	....	....	X	....
Compass-plant (*Silphium laciniatum*)	X	....	....	....	X	....
Greenbriar (*Smilax tamnoides*)	X	X	....	....	X	....
Horse-nettle (*Solanum carolinense*)	....	X	....	....	X	....
Black Nightshade (*Solanum nigrum*)	....	X	....	....	X	....
Goldenrod (*Solidago* sp.)	X	....	....	....	X	....
Milo (*Sorghum* sp.)	....	....	X	....	X	....
Coralberry (*Symphoricarpos orbiculatus*)	X	X	....	....	X	X
Wheat (*Triticum aestivum*)	....	....	X	....	X	....
Grass (unidentified)	X	....	X	....	X	....
Ironweed (*Vernonia Baldwini*)	X	....	....	....	X	X
Winter Grape (*Vitis vulpina*)	X	X	....	....	X	X
Corn (*Zea Mays*)	....	....	X	....	X	....

Even though some individuals exhibited preference for the fruit, the leaves were preferred as a general rule. Leaves lose most of their water content and become brittle rather quickly. They are stored in a tight compact bundle, and the rat feeds while on a platform beside the food store. Occasionally, small amounts of food are eaten at the nest chamber as indicated by discarded pieces around the opening. In every case observed, the food store, if in a stick house, was placed in the upper part while the nest chamber, situated closer to the base, had added protection from inclement weather.

In several kinds of plants for example, wild plum, both fruit and seed are eaten. Probably the same is true of most seeds enclosed by a fleshy fruit. The fruits of climbing bittersweet and grape are widely sought after, but their occurrence is sporadic and they are important only under local conditions. The large "beans" of honeyshuck trees are abundant near some houses on the study area, yet they are not used to the extent that their abundance might indicate.

Goldenrod, ironweed, compass-plant, fragrant sumac, and lamb's-quarters and especially ragweed, seem to be unpalatable and are only occasionally utilized. Even though they may be locally abundant, usually only a single plant or a few leaves are found and they have never constituted the bulk of a food store.

Woodrats were found living where oak trees were common only in the Flint Hills. From the number of opened acorns around several houses in Riley and Marshall counties, I concluded that these woodrats rely heavily on oak mast. Small berries such as those from poison oak, dogwood, and wild grape are most often brought to the house in clusters instead of individually. One house yielded approximately one-third of a bushel of poison oak berries.

A few blades of grass in a food store near the abandoned quarry on the Reservation constitute my only record of this woodrat utilizing native grass. Vorhies and Taylor (1940:513) noted similar scarcity of grass in the diet of *N. albigula* in Arizona. However, Murphy (1952:210) thought that the early summer diet of *N. f. osagensis* in Oklahoma was mainly grass.

There are reports of other species occasionally feeding on insects (Linsdale and Tevis, 1951:296 and Vorhies and Taylor, *op. cit.*: 501). The wings, parts of the head, and the thorax of a cicada found on the feeding platform of a house dismantled in November, 1953, constitute my only evidence of a woodrat feeding on animal matter. Vorhies and Taylor (*loc. cit.*) found that cicadas constituted over half of the total percentage of animal matter in the diet of the white-throated woodrat in Arizona. Murphy (*loc. cit.*) found animal remains (scorpion, snail, and grasshopper) in three of several stomachs he examined.

Food preferences are not clear-cut for this animal. The favorite food of one population may not be used at all by a population in another locale. Woodrats that construct houses at or near osage orange trees usually eat leaves and fruit of this tree instead of any other plants that are available, but exceptions have been noted. A case of unusual selectiveness by the occupant of a house was observed in Greenwood County in July, 1954. The house, situated in a hedge row, was dismantled and found to contain a large store of honey-shuck "beans." This food even though it may be abundant is usually not preferred if products of osage orange trees are readily available. The food store of another house that was built at the base of an osage orange tree in a hedge row consisted entirely of the spikelets of wheat which was growing adjacent to the row. On another occasion, a dismantled house contained large amounts of milo which was growing in an adjacent field. In no instance was there any evidence that woodrats were significantly damaging cultivated crops. In some instances woodrats become pests when living in the vicinity of human dwellings by removing stored products such as fruit and nuts.

One large house contained approximately one bushel of osage orange leaves, some attached to twigs, and approximately 30 "hedge balls."

On July 23, 1952, a male when released from a live-trap went directly to a ragweed plant and ate one leaf. Then he investigated a dogwood seedling, a coralberry plant, and a white snake-root plant without eating any of them. This was the only instance in which ragweed was known to have been eaten even though it was abundant in the vicinity of several houses.

Seemingly, woodrats need green plant material for nutritional purposes other than water content. An adult male kept for four days in captivity was provided water which he frequently drank. Sunflower seeds and chick scratch were provided. When released at his house, he almost at once began foraging several feet from the house even though it was daytime. A rabbit that had been utilizing the house as shelter ran out and stopped approximately 10 feet from the house. The woodrat advanced to within two feet of the rabbit, paused to eat small berries fallen from dogwood trees and, seeming to be completely oblivious of the rabbit, clipped a small dogwood seedling approximately 15 feet from the house, stuffed it into his mouth, and ran back to the house.

Woodrats also exhibit preference among plants of the same kind. A female released from a live-trap on May 20, 1951, went directly to a dogwood seedling six inches in height. Similar plants were abundant around the trap. She smelled the plant but took another one a few inches away. Similar selective behavior has been observed several times in rats which rejected one plant and took another that was not appreciably different to the observer.

Usually a woodrat obtains its food within a few yards of the house. Accessibility of desired food items is one of the most important factors in determining whether or not a house is continually occupied by a succession of woodrats, over a long period of time. One house at the outcrop was in a good location and well protected by a large over-hanging shelf of rock. When found soon after the beginning of my study, the house was obviously not new judging from its large size and amount of litter around entrances. Approximately 30 feet along the outcrop from this house and 15 feet down the hillside, there was a small thicket of wild plum. Although the crop was poor in the dry years of 1952, 1953, and 1954, woodrats had previously relied heavily on this fruit as food, and there were large quantities of opened pits around the above house. In addition, a large wild grape vine grew at the outcrop at one end of the house and there were several bittersweet vines within a few feet. The excellent location and the proximity of highly preferred food items undoubtedly contributed to the success of this house.

Considerable distance is occasionally traversed in order to obtain a desired food item. At one house the minimum distance traveled to obtain corn was 150 feet.

Woodrats have often been observed carrying food material to their houses after they were released from live-traps. Usually, if a weed was the desired item, the rat quickly cut the stem a few inches from the ground. The rat sometimes stood on its hind legs and clipped off the top portion. With the aid of the front feet, the plant was grasped securely in its mouth, and with its head thrown back, the rat carried the food item back to the house. Another procedure when gathering foliage is to fold the material into a more compact bundle by adroit manipulation with the front feet and mouth. When the bundle is of sufficiently small size, it is grasped in the mouth and carried into the house.

Captive woodrats used the front feet and nose to compact the food into the store pile. Small objects such as seeds or small berries are carried several at a time by filling the mouth to capacity. When the rat is eating, it holds the food in the front feet, taking small bites and chewing rapidly. While eating, the woodrat is remarkably dextrous with the front feet, holding the food firmly by appressing the four toes against the palm in much the same manner as a human would grasp an object if he lacked the opposable thumb. The food is held with both forefeet or only one and can be turned to any desired position with no difficulty. While eating, the woodrat maintains a sort of half-crouched position resting on the hind legs and using the tail as a prop.

Occasionally in the course of gathering food, a woodrat may stop for short periods to feed while away from home. Vestal (1938:27) found that *Neotoma fuscipes annectens* Elliot, in California feeds away from the house at night. Observations made on a female and her two young at night with the aid of a red light indicated that each animal alternated in periods of active foraging, eating from the food store, and resting in the nest which was in a building where it could be readily observed. Periods of feeding at the food store lasted up to ten minutes and were sometimes repeated within an hour.

In no instance did I find that woodrats had caused pronounced damage to surrounding vegetation such as the girdling of shrubs and small trees by rabbits and meadow voles. Along the outcrop on the study area, the spread of the hackberry tree is probably retarded to a slight degree by woodrats clipping shoots less than one year old. Conversely, in other situations, woodrats may actually aid in plant propagation by serving to spread seeds to more favorable locations. Dickens (1928:7) in discussing the forest situation in Kansas, attributes new generations of hardwood trees such as oaks and walnuts, to squirrels and woodrats, in that acorns or walnuts, forgotten or neglected, crack by winter freezing and sprout in spring. However, in most instances, the effect of man and domesticated animals upon vegetation overrides and masks any effect attributed to woodrats.

More subtle changes caused by woodrats which are difficult to detect and interpret do occur and influence community activity to some extent. Smooth sumac commonly grows around the margin of woodrat houses and sometimes up through a portion of the house or even surrounds the house with a small thicket. Probably these plants grow from uneaten seeds brought in by the woodrat as food and discarded along with other debris. This increase in plant cover furnishes temporary shelter for other species of vertebrates such as the cottontail. Increased humus resulting from discarded parts of food items and also by falling leaves of surrounding plants, attracts seed-eating and insect-eating birds. Reptiles including small snakes and box turtles sometimes seek shelter in the tangles around woodrat houses.

Probably the white-footed mouse, *P. leucopus,* is the most important competitor for food especially along outcrops which provide favorable habitat for the mouse. This mouse is a seed eater and stores quantities of food (Allen, 1938:406; Burt, 1940:23). It was the most numerous vertebrate cohabitant of the woodrat along parts of the outcrop on the study area. Besides competing with the wood rat in gathering food it probably actually steals from the food stores, because it commonly uses houses of the woodrat as shelter. If present in larger numbers, it could have detrimental effects on woodrats which under local conditions rely on foods (seeds, nuts, etc.) other than leafy parts.

Competition between individual woodrats is probably most intense among animals occupying outcrops when such foods as bittersweet or grape, which ordinarily are not abundant, are preferred food items. Weaker individuals can subsist on other foods and it is not likely that permanent harm to the colony would occur. Only in the case of an extreme shortage of food would intraspecific competition for food be serious. Such competition has not been observed. Availability of house sites, and psychological traits associated with special relationships seem more important than competition for food in determining population size.

BEHAVIOR

Temperament and Sociability

Captive woodrats are generally hostile in their demeanor toward humans. Individuals may become more mild tempered after a lengthy period of confinement, but they always remain unpredictable. Murphy (1952:209) noted similar behavior for *N. f. osagensis* in Oklahoma. Attempts to tame woodrats reared from birth in captivity have been unsuccessful. Captives have been induced to take food from the fingers as it was offered to them through the wire of the cage. However, occasionally they would attempt to bite. One month elapsed before a captive subadult male would accept food from the hand of the observer without attempting to bite.

A captive juvenal female weighing 64 grams and estimated to be four to five weeks of age attempted to bite when I placed food in the cage. After three months she had become even more contentious and although humans were about almost constantly, she never exhibited any degree of tameness throughout the year of her captivity. Her aggressiveness was more apparent than that of the male.

Individuals of both sexes handled in the field varied in temperament from extreme passiveness to extreme viciousness. Some offered little resistance to being handled; others struggled until they were nearly exhausted. Such a rat resisted handling by rapid defecation, urination, squealing, and clawing with the hind feet. Any object within reach of the mouth was grasped and chewed vigorously. On several occasions the rats handled have fought so energetically that when released, they were too exhausted to seek shelter immediately. Other individuals seem to enjoy being handled.

Male woodrats are usually antagonistic toward other males. When the cages of two, one much the larger, were placed together, the smaller more aggressive one immediately sprang against the wall of his cage attempting to reach the larger male. Both would lunge at each other clawing viciously at the wire separating them. When both were placed in the same cage, they slowly approached, touched noses and began fighting. The smaller gained the advantage momentarily, attempting to bite the other's neck. While fighting, both squealed loudly. Several times both would rear up on the hind legs and weave back and forth. During pauses they stared intently at one another chattering their teeth. In a fighting stance commonly assumed, the rat rested on the hind legs, while biting, and while lashing with the front feet. This latter action probably produces the tears so frequently observed in the ears. Practically all old adult males have several tears in one or both ears. A few old large males had the margins of the pinnae so torn as to appear scalloped. Young males before their first season of breeding rarely have torn pinnae. Small scars or wounds on the muzzle, lips, feet, and tail are probably inflicted by claws when the rats are fighting.

When the smaller of the two males was placed in one compartment of a double wire-cage separated by a sliding door from an adult female he exhibited the same belligerence and persisted in attempting to attack, until he finally gained entrance to the female's compartment in the night and killed her.

Hamilton's (1953:182) and Pearson's (1952:463) accounts suggest that the subspecies, *N. f. floridana*, may be more mild tempered toward their own kind than this subspecies. Pearson (*loc. cit.*)

described two adults and six young living together in harmony. Hamilton (*loc. cit.*) mentions conflicts between individuals but such hostility was of short duration.

Communication

Vocal sounds are rarely made except when in distress. A woodrat being handled frequently emits a succession of high pitched squeals each of which may be of three or four seconds duration. On several occasions, a soft plaintive whine varying in pitch has been heard coming from a house. When the ear or toe is clipped a woodrat often emits a short, sharp, "scream." New born young are capable of emitting scarcely audible, high pitched "peeps." Woodrats that are fighting usually squeal loudly.

The most characteristic sound produced by this woodrat is thumping of the hind feet, a reaction that is developed early in life. The rate and intensity of the thumping varies individually and also according to the degree of disturbance. Both feet or only one may be used in producing this sound. When greatly disturbed, rats have been observed to raise the entire rear part of the body from the substratum and stamp the feet forcibly. Seemingly this thumping is a reflex and not a voluntary means of communication as suggested by Vorhies and Taylor for the white-throated woodrat (1940:471). It seems to serve chiefly as a warning evoked by fear or anger, comparable to the behavior of a rattlesnake vibrating its tail. A male woodrat usually begins thumping when it meets another male. The posture, facial expression, and ruffled fur between the shoulders are all indicative of anger. On the other hand, thumping that usually commences when an investigator approaches a rat in a live-trap suggests a fear reaction. Rats usually withdraw into the nest box as far as possible and curl up with the head hidden. In still other instances, the behaviorism suggests that the rat is merely annoyed, as when a captive, engaged in an activity such as feeding or arranging the nest, thumps at a person approaching the cage but without stopping its activity.

Rattling of the tail, highly developed in the dusky-footed woodrat (Linsdale and Tevis, 1951:234-240 and Vestal, 1938:3-6), has been heard only once in the present study. A male caught on July 15, 1952, dashed out of the nest box into the wire trap as I approached. In addition to thumping the hind feet, he vigorously vibrated his tail on the bottom of the cage. Preceding combat with another male, one sharply struck the bottom of the cage with the tail several times but it did not vibrate the tail.

Development of Senses

Although hearing is acute, this woodrat seemingly is unable to recognize certain sounds indicative of possible danger. The cry of a nearby red-tailed hawk, heard several times as a woodrat was released from a live-trap, elicited no response. Sudden nearby noises such as rustling of leaves or sticks will cause a woodrat to be on the alert instantly. Abrupt noises to which captive woodrats are unaccustomed cause them to jump.

Lindale and Tevis have suggested (*op. cit.*:255) that the eye of a woodrat is adapted to arrhythmic activity rather than strictly diurnal or nocturnal activity. On many occasions, woodrats released in broad daylight proceeded directly to the nearest shelter even though such shelter was several feet away. Repeated observance of this reaction has led to the conclusion that sight must be well-developed in order for them to travel so rapidly over such a direct route. If an observer moves slowly synchronizing his movements with those of a woodrat, it is not able to detect his presence. However, the woodrat instantly perceives any sudden movement if the rat itself is motionless. At night a woodrat may rely more on other senses such as touch or smell when it is active.

Woodrats both in captivity and in nature have been observed many times smelling various objects or "testing" the air. Strange food given to a captive woodrat is always smelled before being eaten. The tip of the nose and vibrissae oscillate rapidly when smelling. Seemingly, the sense of smell is well-developed and is useful in choosing food, recognizing other woodrats, and possibly detecting enemies.

Tactile sense is especially well-developed in this animal. Seemingly touch is most acute on the vibrissae, of which, the longest extend beyond the width of the body. Tactile response is also elicited when various other parts of the body are touched. If a rat's abdomen is touched while the animal is being held, the rear feet are brought up and tightly appressed against the abdomen. The hairs on the margin of the pinnae are especially sensitive. Usually the ear is instantly moved and frequently the entire head is jerked around toward the source of stimulus. Blowing on the face is irritating to most rats and they usually react by moving away.

In captivity extremely bitter foods such as cranberries were eaten eagerly even though the rats were not suffering from hunger. Woodrats are generally attracted by sweet foods; however, salt was eagerly licked from a soda cracker by a male in captivity.

Sanitation

This woodrat is sanitary in its habits. Captive animals always choose a particular site, usually a corner of the cage, for defecating and urinating. Feces are rarely found scattered about in the stick houses. There are usually one or more sites where the occupant habitually defecates. Along outcrops droppings are easily detected and have never been observed scattered randomly.

Care of Pelage

Woodrats give much attention to their pelage. When the underparts are being cleaned, the woodrat rests on the hind legs and the base of the tail. The fur is licked vigorously and the front feet are used to part the hairs for more efficient cleaning. As the skin is loose, the front feet are used to pull areas that are not readily accessible within reach of the mouth. The characteristic procedure in cleaning the face is to lick the front feet and rub them over the head in a circular movement. A young woodrat only 15 days old was observed cleaning its face with the characteristic circular movements of the front feet. Its movements were awkward and it lost its balance and fell forward. The tail is cleaned as rigorously as are other parts of the body. It is grasped with the front feet and turned from side to side while being cleaned. After defecating, captives have frequently been observed to bend, with the head between the rear legs, and clean the anal area.

An adult female observed on June 18, 1952, dusting at a small sandy spot three feet from her house, rolled on her back and left side, vigorously wriggling in the sand. After pausing a few seconds to clean her face, she repeated the procedure before returning to the house. This was the only instance recorded of dust bathing, but dusting spots that evidently were used similarly have been observed near many houses. Probably dusting is usually done at night.

INTERSPECIFIC ASSOCIATIONS

General Considerations

The relation of the woodrat to other animals of its environment may be broadly divided into commensalism, parasitism, predation, and competition. Competition may involve either food or space. Some associations are intimate and of great importance whereas others are casual. Intimate associations are exemplified by a rattlesnake living at an outcrop inhabited by woodrats and preying on them, or by fleas living on the rat. Birds foraging around a woodrat house or skinks seeking temporary shelter in it provide examples of casual associations.

Associates are arranged systematically as parasites, predators, and commensals. When a species fits more than one of these categories it is discussed from both standpoints but listed in the category where it is believed to exert the greatest influences.

Parasites

Several specimens from various localities were critically examined for helminths but none was found. Murphy (1952:213-216) found five kinds of helminth parasites, three nematodes (*Longistriata neotoma* n. sp., *Bohmiella wilsoni, Trichuris muris*), and two cestodes (*Andrya* sp. and *Taenia taeniaeformis* larvae) in 50 woodrats (*N. f. osagensis*) examined from Payne County, Oklahoma. He stated that previously only a single species of internal parasites had been reported from this species of woodrat. Most of the woodrats handled in my own study were those on the area where intensive population studies were being made, and they could not be sacrificed. Much more information was obtained concerning external parasites, because they can be in most cases easily observed and collected even on a live animal. In the course of study, one species of tick, three species of fleas, 12 species of chiggers, and one dipteran fly were found parasitizing woodrats. Only the chiggers were found in heavy infestations, and there was never any indication that infestations were fatal.

Warbles

A male woodrat live-trapped on the study area on May 20, 1951, had a large warble on the underside of his neck. This was the first time this parasite was observed on woodrats of the study area even though Dr. Henry S. Fitch had been trapping woodrats on the Reservation since 1948. In 1951, only two other instances of warble infestation were recorded, one in September and one in November. On July 12, 1952, an adult male with a large warble on the throat was live-trapped. The animal was brought to the laboratory and placed in a cage set over a tray of loose soil. On July 19, 1952, the larva was found to have emerged. It was placed in a glass jar containing sand. Approximately two weeks later the adult fly had emerged and was found dead. Several other attempts to obtain adults failed. The fly was identified as *Cuterebra beameri* Hall, by Dr. Curtis W. Sabrosky. This fly was described as new from adults reared from warbles that had emerged from woodrats (*N. f. osagensis*) collected in Greenwood County, Kansas

(Hall, 1943:25-26). Beamer, Penner, and Hibbard (1949:49) found that the eggs of this fly were laid at random around the entrances of the woodrat houses; infestation occurred when the woodrat came into contact with an egg, which stuck to the fur. They observed that captive females each laid approximately 285 eggs.

Of the 105 woodrats live-trapped, 17 (16.2 per cent) were recorded as infested with warbles. Beamer, Penner, and Hibbard (*op. cit.*:47 and 50) collected 72 woodrats from Greenwood County and 13 per cent were infested. Linsdale and Tevis (1951:163) found 94 or 43.5 per cent of 216 *N. fuscipes* live-trapped were infested. Vorhies and Taylor (1940:509) found eight per cent of 275 *N. albigula* examined in Arizona infested. Murphy (1952: 216) found eight per cent (4 of 50) of the *N. floridana* that he examined in Oklahoma to be infested. Linsdale and Tevis (*loc. cit.*) examined the 216 woodrats 2,213 times and recorded an eight per cent infestation. In this report, the 105 woodrats were examined 660 times and warbles recorded 31 times or 4.6 per cent of the time. Woodrats collected by me in other parts of eastern Kansas were seldom found with warbles.

In one infestation, four warbles were present, but in every other instance there was only a single warble. In one instance, an adult male became infested twice in the same season. On August 18, 1952, a large warble was observed on his chest. The rat was again caught three days later and the warble was removed. On October 18, 1952, another small warble having an entrance hole measuring one millimeter in diameter, was observed on the underside of the lower jaw 20 millimeters from the mouth. One week later the swelling was 20 millimeters high, the hole was three millimeters in diameter, and the larva seemed nearly ready to emerge. No sign of its presence was detected when the woodrat was caught one month later.

Of the woodrats infested, 71 per cent had the warbles on the throat, which also was the most common site of infestation reported by Vorhies and Taylor (*op. cit.*:508) and by Linsdale and Tevis (*op. cit.*:167). The other sites of infestation observed were: behind the ear; on the underside of the jaw; on the chest between the front legs; on the front legs; on the belly; and immediately below the eye. An adult male live-trapped November 11, 1951, had a hole 12 mm in greatest diameter on the left side of his face, where a warble had emerged. The hole was only five millimeters from the eye, which was almost closed by swelling; vision probably was impaired. The center of the hole contained dried black substance. When the rat was recaptured 21 days later no visible sign of the warble or its effects remained.

Of the numerous *Peromyscus leucopus* live-trapped on the study area none was found to have warbles even though many were living in or near woodrat houses. *C. beameri* may be host specific for this woodrat. Warbles were observed in May, June, July, August, September, October, and November. The peak of infestation occurs in July and August. More warbles were recorded in 1952 than in 1951, 1953, and 1954 combined. The April-September period of 1952 was the driest on record. The 1952 precipitation for the Lawrence area was 11.60 inches below average. In 1951 precipitation was 15.28 inches above average and only three woodrats were recorded with warbles. These data seem to indicate that warble infestations are more prevalent in periods of dry weather. Of the woodrats infested, seven were adults, six were subadults, and four were juveniles. More females (11) than males (6) had warbles.

The warble fits the description of Linsdale and Tevis. Hair was always missing around the site of the warble and seemingly this is not because of scratching but is caused by the parasite. The warble in nearly every case observed pulsated and exuded a dark sticky liquid. On June 2, 1953, a female that was caught had a warble on her throat. The hole was only one millimeter wide, but there was already a bare spot around the hole 16 millimeters in diameter. The hair begins to fall soon after the warble enters. A warble in the neck of an adult male, and near time of emergence was extracted with considerable effort by grasping it with a pair of heavy blunt forceps and exerting a steady pull. This extraction did not seem to be painful to the woodrat. The hole left was seven millimeters in diameter. The warble was 24 millimeters long and 13 millimeters wide when expanded. Another warble removed from a female August 15, 1953, measured 30 millimeters long and 13 millimeters wide, and the hole it left was eight millimeters in diameter. In this instance also there seemed to be no pain associated with the removal of the warble. The sides of the hole left by the warble soon dry and harden with a black scabby surface. The wound heals rapidly and hair grows back so that within a few days there is no visible sign that the woodrat had carried a warble. For the most part, the woodrat and this parasite are well-adjusted. Nevertheless, an adult female having a large warble on the throat obviously near time of emergence when she was live-trapped on September 23, 1951, died in captivity on October 5. The decayed remains of the parasite were found in the cavity and the adjacent flesh was yellowish and moist indicating an infection. This rat was carefully autopsied but no other possible causes of death could be found.

Fleas

Three kinds of fleas were found on woodrats: the histrichopsyllids *Conorhinopsylla nidicola* Jellison and *Epitedia wenmanni* (Rothchild) and the dolichopsyllid *Orchopeas sexdentatus* Baker.

More males than females were found with fleas. This is possibly a result of a greater wandering tendency among the males. Fleas were observed on woodrats in every month, but were noted more commonly in May, June, July, August, September, and October. Fewer cases of flea infestation were observed in the wet year of 1951 than in the dry year of 1952. In May, 1952, live-trapped woodrats of all age classes were noted to be more heavily infested with fleas than those taken in the same month of the previous year. This trend continued for the remainder of 1952 (Table 6), and into 1953.

The species *C. nidicola* was described as new from specimens taken from woodrat nests six miles north of Lawrence, Kansas (Jellison, 1945:109). A fourth flea, *Epitedia neotomae,* described as new in 1946 was collected from woodrat nests five miles north of Lawrence and was also taken at the type locality from a spotted skunk, *Spilogale putorius* (Linnaeus), (Jameson, 1946:62-64). However, this flea was not found in my study.

Most of the rats live-trapped on the study area were infested with *O. sexdentatus,* and *C. nidicola* was found there only once. However, in nest material from houses dismantled approximately one mile from the study area, all three kinds were found. One nest contained 100 per cent *C. nidicola.* Another contained 95 per cent *C. nidicola,* four per cent *E. wenmanni,* and one per cent *O. sexdentatus.* There were many fleas in the nest and hundreds of flea larvae. A female rat caught in a snap-trap from one of the houses had six *E. wenmanni* and three *C. nidicola* on her when examined. The procedure to obtain fleas from dead woodrats was to place the animal in a plastic bag along with some paradichlorobenzene crystals as soon as it was removed from the trap. In this manner fleas would be killed, drop off the host, and could easily be found in the bottom of the sack.

It seems that the different kinds of fleas have different preferences in the times chosen to attack the host. *C. nidicola* seemingly prefers to feed by day while the woodrat is in the nest and is not regularly carried about when the host leaves the house, but

O. sexdentatus stays on the rat and is not regularly found in the nest. Possibly different kinds of fleas are dominant in different locales.

TABLE 6. A COMPARISON OF FLEA INFESTATION BETWEEN THE WET YEAR OF 1951 AND THE DROUGHT YEAR OF 1952.

Month	Number infested		Number live-trapped		Per cent infested	
	1951	1952	1951	1952	1951	1952
January	......	1	......	6	0	17
February	......	......	......	6	0	0
March	......	1	8	11	0	9
April	......	3	10	16	0	19
May	1	6	12	12	8	50
June	2	10	13	10	15	40
July	1	5	11	14	9	36
August	......	4	......	20	0	20
September	1	6	10	9	10	67
October	5	4	10	5	50	80
November	......	3	7	5	0	60
December	......	1	7	3	0	33

Even though the number of fleas carried is usually small, these parasites must cause great annoyance to the woodrats, which are continually exposed to their attacks. When concentrations in the nest are heavy, damage to young animals might be considerable. I found no evidence that fleas were directly responsible for the death of an adult.

Of the woodrats live-trapped each month (1951-1954 inclusive), the percentages infested with fleas were as follows: January, 18 per cent (of 11); February, 11 per cent (of 9); March, 6 per cent (of 18); April, 13 per cent (of 23); May, 44 per cent (of 25); June, 44 per cent (of 61); July, 27 per cent (of 22); August, 31 per cent (of 26); September, 54 per cent (of 24); October, 64 per cent (of 14); November, 31 per cent (of 16); December, 9 per cent (of 11).

Chiggers

Chiggers are more numerous on woodrats than are any other ectoparasite. In the course of the study, the chiggers collected from woodrats of the study area were of the following ten kinds: *Trombicula lipovskyi* Brennan and Wharton; *Trombicula sylvilagi* Brennan and Wharton; *Trombicula alfreddugèsi* (Oudemans); *Trombicula lipovskyana* Wolfenbarger; *Trombicula trisetica* Loomis and Crossley; *Euschöngastia peromysci* Ewing; *Euschöngastia diversa* n. sp. Farrell (in press); *Euschöngastia setosa* (Ewing); *Pseudoschöngastia farneri* Lipovsky; *Pseudoschöngastia hungerfordi* Lipovsky. Also, *Trombicula cynos* Ewing from a woodrat taken on another part of the Reservation, and an unnamed species of a genus shortly to be named by Lipovsky, Crossley, and Loomis (in press) from nest material were reported to me by Dr. Richard B. Loomis.

Chiggers were collected in two ways. Most were scraped from the animals where they were grouped in clusters. A second more efficient but more time-consuming method was to place a wire bottomed cage over a large pan of water containing liquid detergent. The woodrat was kept in the cage for two to three days and the chiggers dropped into the water. The detergent prevented them from floating and they could be collected by decanting the water.

Chiggers were observed on the woodrats only when they were present in clusters or in large numbers scattered over the body. The most common site of attachment in winter was in the ear. In most cases clusters were present in both ears but sometimes they were in only one. Other sites of attachment, in order of decreasing preference, were: underside at base of tail; around vaginal orifice; at the bases of teats; inner surfaces of hind legs; on hips and rump; around anus; on scrotum; between the shoulders; and on lower jaw.

Chigger clusters were observed mostly in late summer, fall, and winter, beginning to appear by August and declining in March. In summer they were rarely observed in clusters. Summer chiggers are present but scattered over the body making them difficult to find and almost impossible to collect while handling the animal in the field. In July, 1952, a male was caught that had a few attached around the anus; however, they were not in a large cluster as seen in winter. In June, 1954, two males were observed with chiggers; one with a few on the scrotum and ear, and the other with one on the ear. *T. alfreddugèsi* and *T. lipovskyana* are the two common chiggers in summer infestation although *P. hungerfordi* and *P. farneri* are occasionally found. The remaining chiggers cause infestations only in fall and winter. Why winter chiggers are found in clusters I do not know. Perhaps inactivity is associated with decreased temperatures.

In five nests examined in February, November, and December, chiggers were less abundant than were fleas. As many as three kinds belonging to two genera have been found in the same cluster. A scraping from the ear of a male on February 8, 1953, had 20 *T. lipovskyi,* six *T. diversa,* three *E. peromysci* in the same cluster. A cluster removed on August 20, 1952, from another male contained 17 *P. hungerfordi,* eight *T. alfreddugèsi,* and two *T. lipovskyana.* In November, 1952, an adult male was placed for three days over water. Four kinds of chiggers were parasitizing this animal. The most numerous was *T. lipovskyi* with approximately 100 being collected. The others, *E. diversa, T. sylvilagi,* and *T. trisectica* were present in smaller numbers.

A subadult male first was observed with a cluster of chiggers in each ear on September 6, 1952. This male was caught several times in July and August, but chiggers were not observed. Chiggers were still present on September 8, October 12, and 25. On November 15, they were scraped from both ears and *T. lipovskyi, T. sylvilagi,* and *E. diversa* were found. Ear scrapings from another male and a female on this same day from the same area both contained *T. lipovskyi* and *T. sylvilagi.* In all three cases *T. lipovskyi* was more numerous than the others. Chiggers had not reinfested the subadult male by November 16 and 22, and in December. The animal was next caught on February 8, 1953, and chiggers were again found in the ears. They were scraped from the right ear and *T. lipovskyi, E. diversa,* and *E. peromysci* found to be present in the same cluster. The rat was captured again on March 14, 1953, but chiggers had not reinfested the ear that had been scraped.

Of the woodrats live-trapped each month (1951-1954 inclusive), the percentages with chiggers were as follows: January, 64 per cent (of 11); February, 33 per cent (of 9); March, 11 per cent (of 18); April, none (of 23); May, none (of 25); June, 3 per cent (of 61); July, 5 per cent (of 22); August, 31 per cent (of 26); September, 67 per cent (of 24); October, 71 per cent (of 14); November, 69 per cent (of 16); December, 64 per cent (of 11).

Ticks

Nymphs and larva of the American dog tick, *Dermacentor variabilis* (Say), were found parasitizing woodrats from the study area. The woodrats were never heavily infested with ticks; the largest number observed on any one animal, 11 total, were on a subadult female, on June 3, 1953. The above mentioned female was caught for the first time on May 28, 1953, at a house constructed at the outcrop, and at that time she had no ticks. She was next caught on May 30, 1953, at the same location, but this time she had two nymphs, one on either side of the nose among the vibrissae. These were removed. On June 2, 1953, she was captured again at the same location but had no ticks. However, on the following day, June 3, she was found in a trap approximately 175 feet along the outcrop at another house and in the night had acquired 11 ticks, 10 nymphs and one larvae. Three were on the pinnae; one on the right and two on the left. The remainder were on the muzzle. This female seemed to be wandering extensively judging from the intervals between captures and probably she acquired the ticks at sites other than her home.

The usual location for attachment was on the pinnae or the muzzle or both. Nymphs were more abundant than larvae. Of the many ticks collected only one was a larva. Ticks were observed more frequently in June, 1953, than any other time in the study. They were found on woodrats only in the months of May, June, July, August, and September. Only 15 different rats were found harboring these parasites in the entire course of study. More males (10) carried ticks than females. Most (11) of the woodrats infested with ticks were living along the outcrop. An exceptionally mild winter following the exceedingly dry year of 1952 may account for the number of ticks observed in June, 1953. The last half of May, 1953, was unseasonably warm, and June was the second hottest on record up to that time. Lack of ticks in 1951 may be correlated with the fact that precipitation was the heaviest since records were begun in Lawrence in 1869.

TABLE 7. WOODRATS RECORDED WITH TICKS.

Date	Sex and age	Site of attachment	Location of house
May 10, 1952	juvenal female	muzzle	woodland
May 11, 1952	adult male	muzzle	woodland
May 18, 1952	juvenal male	muzzle	woodland
June 28, 1952	adult female	unattached	outcrop
July 31, 1952	subadult male	on shoulder	outcrop
August 20, 1952	adult male	muzzle	outcrop
May 28, 1952	adult male	muzzle	outcrop
June 3, 1953	juvenal female	ear and muzzle	outcrop
June 3, 1953	subadult female	ear and muzzle	outcrop
June 5, 1953	adult male	muzzle	woodland
June 5, 1953	adult male	muzzle	outcrop
June 7, 1953	subadult female	muzzle	outcrop
September 10, 1953	adult male	muzzle	outcrop
June 21, 1954	adult male	ear	outcrop
June 21, 1954	adult male	muzzle	outcrop

Predators

The removal of only a few woodrats from a colony when it is at low ebb would compound the struggle toward increasing numbers of woodrats again. Woodrats that dwell at outcrops are possibly more protected from enemies than are those that live in more open situations. The woodrat is able to carry on all of its activities without having to stray from the outcrop more than a few feet. At almost any time that an enemy is encountered, the woodrat has ready access to many deep crevices and fissures and only a few enemies can pursue the woodrat into such retreats.

On the Reservation and nearby areas, the pilot black snake (*Elaphe obsoleta*), timber rattlesnake (*Crotalus horridus*), horned owl (*Bubo virginianus*), long-tailed weasel (*Mustela frenata*), and spotted skunk (*Spilogale putorius*) are considered to be by far the most important natural enemies. Relationships of each of these predators to the woodrat are discussed in a separate paper (Fitch and Rainey, 1956). Various other predators take woodrats occasionally, and their combined effect is probably important, especially when the population of woodrats is low.

Blue-racers (*Coluber constrictor*) observed in this area were not large enough to overcome an adult woodrat. Newborn woodrats might fall prey to blue-racers. On one occasion, a young blue-racer approximately 10 inches in length was observed sunning itself on a woodrat house. When disturbed it sought shelter by crawling in among the sticks of the house. These snakes have been seen frequently utilizing the shelter of brush piles similar to those in which woodrats commonly construct houses. In most localities, however, the habitats of the blue-racer and the woodrat overlap but little.

Large bull snakes (*Pituophis catenifer*) may prey on woodrats, at least occasionally, where the rats live in hedge rows or open woodland. Bull snakes of all sizes have been seen both along the outcrop and in woodland although the species is more characteristic of grassland. Snakes that prey on woodrats would be able to pursue the animal into most burrows or crevices and kill it by constricting or pressing it against the sides of the burrow. The species was listed by Vorhies and Taylor as an important enemy of the white-throated woodrat in Arizona (1940:508).

Copperheads (*Agkistrodon contortrix*) are fairly common along the outcrop. However, woodrats were not represented among several dozen recorded food items from the Reservation, and must be eaten only rarely if at all. Adult rats are too large to be swallowed by any but unusually large copperheads. On September 30, 1951, a large copperhead was coiled on top of a woodrat house at a rock fence, and a live-trap only two feet away contained a rat. However, neither the snake nor the rat evidenced interest in the other.

Dr. Rollin H. Baker told of seeing on May 1, 1948, a Cooper's hawk (*Accipiter cooperii*) at the Reservation part of the eastern section of outcrop, flying off with a woodrat. The hawk dropped the rat, which was found to have been killed by having the back of the skull crushed.

The red-tailed hawk (*Buteo jamaicensis*) is one of the most abundant hawks on the study area and throughout eastern Kansas. It has been observed hunting over open and woodland situations of the study area as well as perched in trees. Fitch (1947:150) found that woodrats (*N. fuscipes*) comprised only about 1.1 per cent of the total weight of the food of this hawk in Madera County, California. The daylight hunting of these and other hawks probably makes them unimportant enemies of the woodrat. The less abundant broad-winged hawk, *Buteo platypterus* (Vieillot), may be more important locally because it is inclined to hunt more in woodland.

Marsh hawks (*Circus cyaneus*) are seen occasionally hunting by flying over open situations on the study area. If a woodrat was discovered in the open in the day, it probably could be captured by a marsh hawk, but such occurrences would be exceptional.

Opossums (*Didelphis marsupialis*) are common on the study area and often disturbed traps in attempts to reach either the bait or the captured rat. Hairs found around or on live-traps torn open in a few cases were identified as those of an opossum. Blood indicated that the rat was captured or at least injured. Sandidge (1953:98) recorded no remains of woodrats in 62 stomachs examined from Douglas County. Fitch and Sandidge (1953:322-323) examined 79 scats from the Reservation but found no woodrat remains. The commensal nature of the relation of opossums to woodrats is perhaps more obvious than that of a predator-prey relation. Opossums are frequently found utilizing occupied woodrat houses as daytime retreats. On December 1, 1951, a young opossum was found in the upper part of an occupied woodrat house. It made no attempt to escape as the house was dismantled. A young opossum was found on June 22, 1952, in a live-trap set at a woodrat house. After it was released, it moved directly into the stick house.

Opossums denning along outcrops inhabited by woodrats compete for space and, in some instances, for food. Sandidge (*op. cit.*:

101) found wild grape in three of the stomachs he examined. Fitch and Sandidge (*loc. cit.*) found wild grape to be the most abundant single item in the scats they examined from the Reservation. Hackberries were second in importance. Both are important food items for the woodrat.

Since this study was begun, raccoons (*Procyon lotor*) have been abundant throughout eastern Kansas. Evidence indicates that this animal might be an important predator in local situations where woodrats were available. On the study area, the raccoon constituted a serious pest in its habit of persistently breaking into live-traps. In the course of the study, marauding raccoons repeatedly made live-trapping so unprofitable that operations were suspended for varying lengths of time. Efforts to protect the traps were to no avail. The frequent occurrence of blood on the trap indicated that the rat had been killed and eaten. Hair, tracks, and scats around the trap revealed the raccoon's identity in several instances. Howard J. Stains studied raccoons for the past several years. He examined 738 scats mostly from west-central Douglas County. Two scats in 14 examined from caves in Barber and Comanche counties in south-central Kansas had remains of woodrats (*N. micropus*), but the scats from Douglas County contained none and he informs me that woodrats are not found in the area, in Douglas County, from which the scats were collected.

Fitch and Packard (1955:212) found remains of only two woodrats in an examination of 118 scats of coyotes (*Canis latrans*) collected on the Reservation over a five-year period. Tiemeier (1955: 202) found woodrats (probably including both *N. floridana* and *N. micropus*) in 11 of 871 coyote stomachs collected throughout Kansas over a six-year period.

Investigators in other locales have found that woodrats of various species are taken frequently by coyotes. Sperry (1941:15) recorded woodrats 355 times (4 per cent) in an examination of 8,339 stomachs from 17 states. He states: "Locally, however, they were an important source of food. For example, the coyotes from Texas derived almost a fourth (24 per cent) of their food from cricetids, four-fifths of which were wood rats. In fact, 40 per cent of the Texas coyotes that ate *Neotoma* took nothing else at their last meal." Linsdale and Tevis (1951:196) state that woodrats rank first among all kinds of food taken by coyotes. They recorded woodrat remains 283 times in examining 980 scats. Vorhies and Taylor (1940:508) state: "Notes and other available records of feces examination place the coyote definitely among the more important enemies of *Neotoma*, while stomach examinations fail to so record it at all." Fitch (1948:74) examined 1,173 scats from the San Joaquin Experimental Range in California and found woodrat (*N. fuscipes*) remains 162 (4.9 per cent) times.

The red fox (*Vulpes fulva*) is not common and the gray fox (*Urocyon cinereoargenteus*) is considered rare in Kansas. Tracks of fox have been seen on the study area. A fox would take a woodrat whenever possible, but this predator is too scarce to be important except perhaps under local conditions.

Escape Reactions

Woodrats, except for young, when forced to leave the house always have predetermined routes of escape. Thorough familiarity with these routes is a definite survival factor. In many cases the reaction is so stereotyped that it can be predicted beforehand. This is more pronounced among rats living in houses constructed at bases of trees. The most common reaction is for the rat to leave the house hurriedly and seek refuge in the tree. Movement is so fast that usually only a flash of brown is seen. The animal invariably stops to survey the situation when it is well up in the tree. If pursuit is continued the rat will move to the uppermost branches or to adjacent trees. If only one tree is available, the rat moves back and forth attempting to remain as far as possible from the pursuer. Footing is always sure, but they have never been observed to make leaps of any great distance from one limb to another. Sometimes the rat seeks refuge in burrows beneath the house. When the house has been partly destroyed, the rat may attempt to leave, and appearing momentarily confused with its surrounding it can be easily captured by hand. Its bewilderment seemingly is due to destruction of its escape routes from the house. Several woodrats attempted to escape from me by traveling on the ground in dense vegetation. However, they immediately took to trees if capture was imminent.

The inability of woodrats to react without hesitation in time of danger when the rats are in unfamiliar surroundings has been observed many times. If released from a live-trap several feet from its house, a rat usually is confused, and frequently seeks any available shelter and remains for several minutes before attempting to return home. Animals traveling across strange territory are circumspect and usually move cautiously with frequent stops. The behavior after release of a subadult male live-trapped on June 24, 1954, is indicative of uncertainty when in strange territory. This male was new to the section of outcrop where he was trapped and probably was a wanderer from outside the trapping area. Instead of running directly to the outcrop after release as resident rats normally do, he ran away from the ledge and took refuge under a large rock. After remaining there for a few seconds, he moved into the open and stayed there for 10 minutes; his only movements were quivering of the vibrissae and slowly turning the head from side to side as though intently studying the surroundings. He then moved toward a rock fence approximately 40 feet away. He did not run but progressed in a slow methodical fashion, pausing periodically to examine the surroundings. He gave the appearance of being thoroughly lost. If a predator had encountered this woodrat, capture would have been almost certain. A rat released in familiar territory always moved rapidly and without hesitation.

Not only are escape reactions a necessity for the individual, but lives of suckling young depend on these predetermined means of escape. The ability of suckling woodrats to cling to the teats of the mother has been described for other species and is no less developed in *N. floridana.* On July 25, 1954, a house constructed in a hedge row was investigated for occupancy. As soon as the house was disturbed a female with three young attached to her teats dashed out and into the tree. Her movement was quick and sure even with the added weight of the young. She would run along limbs from one part of the tree to another attempting to avoid capture. The young were dragged on their backs over the sharp spines with no apparent injury, and when one of the young lost its grip the mother immediately grasped it in her mouth and carried it in this fashion.

Even where trails are not visible, rats behave in a manner that indicates familiarity with their surroundings; those repeatedly live-trapped at the same site tended to react similarly after each release. The speed of their movements indicates that the escape routine involves conditioned reflexes; it could not be accomplished so efficiently without previous learning. Movement to shelter is direct and not erratic. The fact that young animals are more reluctant to leave a house and are hesitant in their movements after having left provides further evidence that escape reactions are learned.

Wounds varying in nature and severity are frequently observed. Some of these may be from fighting and others may result from encounters with predators. All of the skin had been torn from the top of the left hind foot of a female examined on April 26, 1952.

The bones of the toes and tendons were exposed, but there was no sign of infection. A female on October 14, 1951, had a deep wound 25 millimeters long and 20 millimeters wide on the right thigh. The wound had an odor of putrefaction. Nearly one month later it was much smaller (five by three millimeters) and healing rapidly. On February 17, 1952, a male was also observed to have a large wound (18 by 15 millimeters) on the right thigh. Still another male on October 12, 1952, had a deep cut one inch in length on the left thigh.

In a female observed on May 12, 1952, an osage orange thorn 15 millimeters long had pierced the left ear to approximately half its length, broken off, and the wound had healed holding the thorn firmly in place. The thorn had entered from the anterior side of the ear. When it was removed, scar tissue adhered to the thorn leaving a round orifice in the pinna. When the rat was recaptured on June 13, 1952, the hole had closed.

Infected lesions have been noted several times on woodrats. A male caught on May 15, 1952, had such a lesion on the lower jaw. Surrounding hair was matted by yellowish exudate from the lesion.

One male was completely blind in the right eye but the cause was not evident. The rat seemed to be well adjusted to partial loss of sight because he stayed in the area 210 days after the initial capture.

Another common type of injury was the partial or complete loss of an extremity. Both males and females were live-trapped with varying lengths of their tails missing. The skin of the tail is easily torn away. The exposed part shrivels and drops off in a few days. The ease with which the skin is lost probably saves many woodrats from predators. Bob-tailed woodrats are not much handicapped by the loss. Individuals have been observed maneuvering with seemingly as much agility as woodrats with normal tails. One female was recorded as having lost a toe on the left hind foot.

Commensals and Competitors

The phase of the study directed toward analysis of house structure and related aspects was done mostly in 1952 and 1953. These years were record breaking drought years and woodrat houses were strongly affected. Houses dismantled in these years reflected the results of many consecutive days without rainfall; fine dust had thoroughly permeated the structure including food stores. Possibly for these reasons, the arthropod fauna inside woodrat houses was smaller than would be expected. A few isopods, moths, caterpillars, and other larval forms have been seen in houses partially dismantled when I was collecting woodrats, but these arthropods were not preserved. Spiders were the invertebrates most commonly found in or on woodrat houses. Other kinds include one hemipteran (*Anasa tristis*), one neuropteran (*Chrysopa* sp.), two coleopterans (*Ptinus* sp. and *Cryptophagus* sp.), and one mollusk (*Stenotrema leai aliciae*). This list of house commensals is far from complete because this phase of study was not investigated in great detail.

Spiders were in nearly all houses dismantled. For some kinds, the stick houses were favorite sites for construction of webs over the surface; others, instead of spinning webs, lived deep within the house. Most abandoned houses soon covered with webs. In fact, the presence of spider webs on entrances is an almost infallible sign that the house is not inhabited by a woodrat. Houses that are occupied never have webs at entrances and frequent addition of sticks, in the course of adding to or repairing the house, usually limit webs to the margins of the base. The following spiders were found in or on woodrat houses: *Herpyllus vasifer, Phidippus audax, Xysticus elegans, Agelenopsis naevia, Micrathena gracilis, Eustala anastera, Lycosa helluo,* and *L. gulosa.* Harvestmen, *Leiobunum vittatum,* are common arachnids in this area and are occasionally seen on woodrat houses.

I found no amphibians in woodrat houses, but Linsdale and Tevis (1951:192) reported three kinds of salamanders and one tree toad from houses in California and Vestal (1938:12) recorded two salamanders and a newt in houses there. The ant-eating frog, *Gastrophryne olivacea,* is sometimes found under rocks on hillsides below rock outcrops inhabited by woodrats.

The box turtle, *Terrapene ornata,* is common on the study area except for that part of it within the Reservation. It was numerous in woodland along the outcrop. A box turtle was in a live-trap at a woodrat house in a brush pile on May 13, 1952; another was in a live-trap on June 21, 1952. After the landowner had burned several of the brush piles containing woodrat houses in the spring of 1954, the shell of a box turtle was found among the ashes of one of the houses.

The five-lined skink, *Eumeces fasciatus,* is the most common reptile on the study area. On June 27, 1952, an adult was seen on a woodrat house into which it escaped. On May 26, 1953, a large male in breeding condition was observed running into a woodrat house. The houses provide the type of shelter required by the skink, which also feeds on the arthropod fauna found around or in the house.

Great Plains skinks, *Eumeces obsoletus,* are common along the ledges and rocky hillsides. On June 25, 1952, a large adult was caught in a live-trap set at a woodrat house. After it was released it disappeared into the house. These skinks are frequently caught in reptile traps placed along the outcrop.

Ring-necked snakes, *Diadophis punctatus,* are common along the ledges and rocky hillsides below. On May 19, 1951, one was seen lying on a rock near a woodrat house at the outcrop. In July, 1948, a class dismantling woodrat houses under the supervision of Profs. Henry S. Fitch and George H. Lowery, Jr., found a ring-necked snake in the damp soil under a woodrat house.

Birds caught in live-traps set for woodrats include: house wren, *Troglodytes aedon;* catbird, *Dumetella carolinensis;* brown thrasher, *Toxostoma rufum;* song sparrow, *Melospiza melodia;* cardinal, *Richmondena cardinalis;* and Harris' sparrow, *Zonotrichia querula.* Even though birds such as tufted titmice, *Parus bicolor;* black-capped chickadees, *P. atricapillus;* and juncos, *Junco hyemalis,* are frequently seen foraging at woodrat houses, other birds are probably attracted by bait at traps. Mourning doves, *Zenaidura macroura;* yellow-billed cuckoos, *Coccyzus americanus;* crows, *Corvus brachyrhynchos;* blue jays, *Cyanocitta cristata;* cardinals; field sparrows, *Spizella pusilla;* and rose-breasted grosbeaks (*Pheucticus ludovicianus*) have been observed nesting on the study area.

Fox squirrels (*Sciurus niger*) are common over all the study area and compete with the woodrat for food, notably seeds of osage orange. Fox squirrels have been seen many times foraging on the ground near woodrat houses. Bailey (1905:108) found a gray squirrel in a woodrat house (*N. f. rubida*) in Texas.

The white-footed mouse, *Peromyscus leucopus,* is the mammal most commonly associated with woodrats in eastern Kansas. This mouse is more abundant along the rock outcrops than around houses in woodland, and is a common commensal and competitor for space. As a competitor for food the mouse is discussed under the section on food habits. A house dismantled in May, 1954, which was occupied by a female and one young male rat, also harbored a white-footed mouse. On another occasion, a *P. leucopus* dashed from the entrance hole of a woodrat house, paused a few seconds, and dashed back into the house when I made a slight movement. As many as three mice have been live-trapped repeatedly from a single woodrat house indicating that they lived there; they would dart into the house after release. On July 6, 1951, an adult female woodrat and an adult female *P. leucopus* were together in a live-trap. The woodrat was in the nest box and the mouse at the opposite end of the trap huddled in one corner. After watching for several minutes, it seemed to me that the woodrat was not antagonistic toward the mouse when a distance of approximately one foot separated them. When the mouse was forced close to the nest-box, however, the woodrat slashed out with the forefeet. The mouse easily avoided the blows and retreated to the far end of the trap again. The woodrat made no attempt to follow up the attack. These observations suggested to me that a white-footed mouse could live as a commensal in a house occupied by a woodrat.

Cottontails, *Sylvilagus floridanus,* employ rock outcrops for shelter. On May 9, 1952, a young cottontail was caught in a live-trap set at a woodrat house built in a brush pile. The following day the same trap had caught another cottontail of approximately the same age. On February 8, 1953, a cottontail was flushed from a woodrat house at the outcrop. On December 1, 1951, a cottontail was flushed from a woodrat house that was being dismantled. At another house, a cottontail was flushed from a large opening in one side for several days in succession, and seemingly, it was using it as a regular daytime retreat. Baker (1942:343) found a cottontail in a house of *N. f. rubida* in Texas. The tangles around woodrat houses or the house itself affords good daytime retreats for the cottontail. Competition for food between these two animals is probably slight.

Short-tailed shrews, *Blarina brevicauda,* woodchucks, *Marmota monax,* and meadow jumping mice, *Zapus hudsonius,* have been observed near woodrat houses.

REPRODUCTION AND DEVELOPMENT

Season of Breeding

In eastern Kansas the season of breeding is from February through August; exceptionally, individuals may breed in September. There are three periods when the incidence of breeding is especially high: late winter (usually early February), late March and early April, and in May. Females that are not fully mature at the onset of the breeding season in late winter may not be bred for the first time until March or April, and females that are not found by a male while they are in heat pass through another complete oestrus cycle before becoming pregnant, thus lagging behind the majority. Chapman (1951:282) reported that *osagensis* in eastern Kansas has spontaneous oestrous cycles of three to eight days which continue throughout the year. Hamilton (1953:181) stated: "The *floridana* group, at least in the southeastern states, apparently breeds throughout the year. . . ."

Indications of Breeding in Males

In some males the testes begin to enlarge in late January, but in others this development is later. Both testes may not increase in size at the same time; frequently one lags behind. The testes of most mature males are fully scrotal in position by February and tend to remain in the scrotal sac while the rat is being handled. Sexual activity does not commence until February. When reduction in size begins, the testes usually pass out of the scrotal sac when handled. They may be manipulated back into the sac by palpating the abdominal cavity. Linsdale and Tevis (1951:354) found that viable sperm in the cauda epididymis of *N. fuscipes* formed a conspicuous bulge and that the testes were scrotal. At the peak of reproductive activity in *osagensis,* this bulge is as much as four millimeters thick. The testes are then fully scrotal and do not slip out of the sac. The testes of males undergo slight changes in size throughout the season of breeding and at times are carried in the abdominal cavity. Males with testes that have regressed in size and withdrawn into the abdominal cavity within the season of breeding probably still are capable of fertile matings. In an old male whose testes slipped easily in and out of the scrotal sac the cauda epididymis of both sides was packed with motile sperm. Both testes were being carried in the abdominal cavity. They were 17 millimeters in length and the bulge formed by the cauda epididymis of both testes when forced into the scrotum was slight. The lull in sexual activity in males corresponds with the periods when many females are pregnant.

By late February the testes of most males are carried in the abdominal cavity. In the latter part of March and in April, testes of males are generally fully scrotal, some attaining a maximum length of 25 millimeters. The testes of some are fully scrotal in early May and are abdominal toward the end of the month. Testes of others are scrotal in late May or early June, but most often they are abdominal in June. Even if the testes are forced into the scrotum, the cauda epididymis does not bulge; absence of a bulge might indicate inability to breed. The testes in some individuals are fully scrotal again in late July and in early August. Relatively few males retain the testes in the scrotal sac into September. Occasionally males breed successfully in September. In the entire season of breeding there are a few at any particular time having their testes in the scrotum. Some young adults do not undergo the frequent cyclic changes in size of testes that older males do.

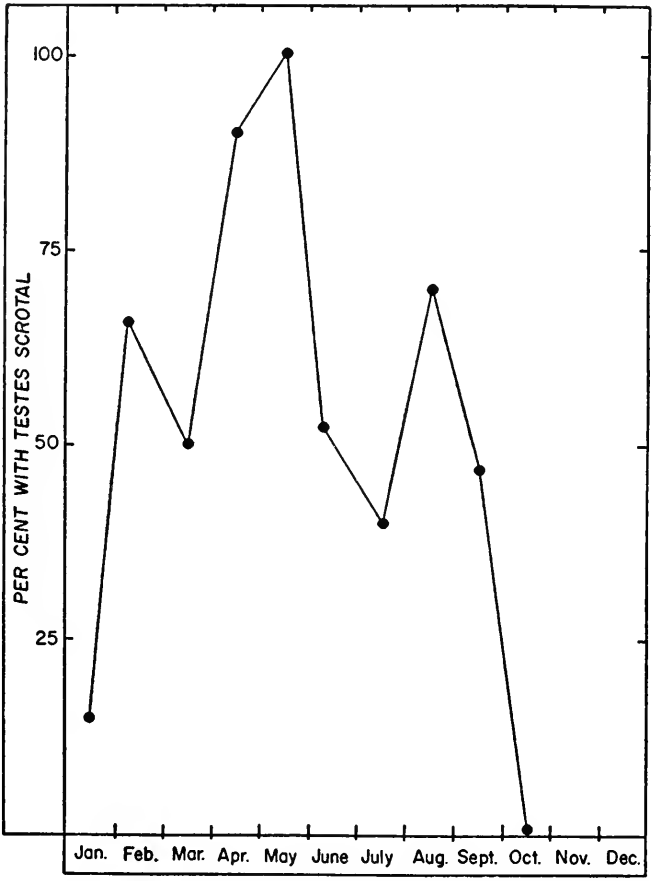


FIG. 3. Record of males with scrotal testes in the period from April, 1951, to June, 1954, represented as per cent of total number of mature males captured.

Reproductive activity among males for the period of study is graphically represented in Figure 3. No significant difference could be detected between successive years.

Sexual maturity develops rapidly in some males, slowly in others. In a young male first captured on July 15, 1952, and then weighing 152 grams, the span of records extended to March 15, 1953, for a total of 243 days. In this period, the maximum weight attained was 250 grams (March 15, 1953), a gain of only 98 grams. In August, 1952, the testes could be located only by palpating the abdominal cavity and were estimated to be four millimeters long. Even in February and up to the last capture when other males were becoming sexually active, the testes of this male remained small, and they were never observed scrotally. Furthermore, he did no wandering in the breeding season. In the local population of adults there were three males weighing approximately 300 grams which were sexually mature. Sexual maturity was not demonstrable among males in their first season. However, there are indications that rats of second litters or even third litters may mature sexually by February or March the following year.

Indications of Breeding in Females

In periods of sexual inactivity, the vagina is closed, externally the teats are small and hard with flakes of loose epidermis on them, the clitoris is white and not swollen, and hair covers the entire abdomen. The horns of the uterus are soft and are not enlarged. The ovaries are flat, small, and bean-shaped, containing only single and double-layered follicles. In females that are in heat the vaginal orifice is prominent, and the clitoris is enlarged becoming inflamed in the later stages. The vulvar lips are turgid and may stand widely apart or may be in contact with each other. The horns of the uterus are enlarged, firm, and pinkish; the ovaries are enlarged, with pronounced follicular proturbances.

Pregnancy is indicated by an enlarging and softening of the nipples, loss of hair in the mammary area in later stages, especially in the mid-line, and thickening and inflammation of the mammary area. The vaginal orifice may or may not be present. The nipples in later stages are distended and sharply pointed. There is a steady increase in weight, the abdomen is swollen in later stages, and the mammary area is noticeably warmer to the touch than other parts of the body.

A sudden weight loss is indicative of parturition (Fig. 4). The skin of the mammary area of females nursing young is devoid of hair, thickened and wrinkled. When the young are unattached, the teats are not distended. Each teat gives the appearance of being sunk into a crater with a wrinkle around it. The tips may be rough to the touch. The teats are flaccid and can be stretched to 15 millimeters or more in length. Frequently, milk can be forced from the nipples.

In late stages of lactation, hair begins to grow on the mammary area especially in the mid-line, the teats shrink to 3-4 mm. and harden; the skin of the mammary area is no longer thickened nor especially warm to the touch, and the vaginal orifice may be open or closed according to the stage of oestrous. Some females breed while still nursing a litter. A female in late lactation, removed from a house in a hedge row on May 16, 1954, had one young, which weighed 61 grams and was approximately one month old. There was a band of new hair growing down the mid-line between the female's teats, the nipples were hard at the tips, and there was a vaginal orifice. There were two swellings in each horn of the uterus which were shown by sectioning to be early embryos. Each of the ovaries had two corpora lutea.

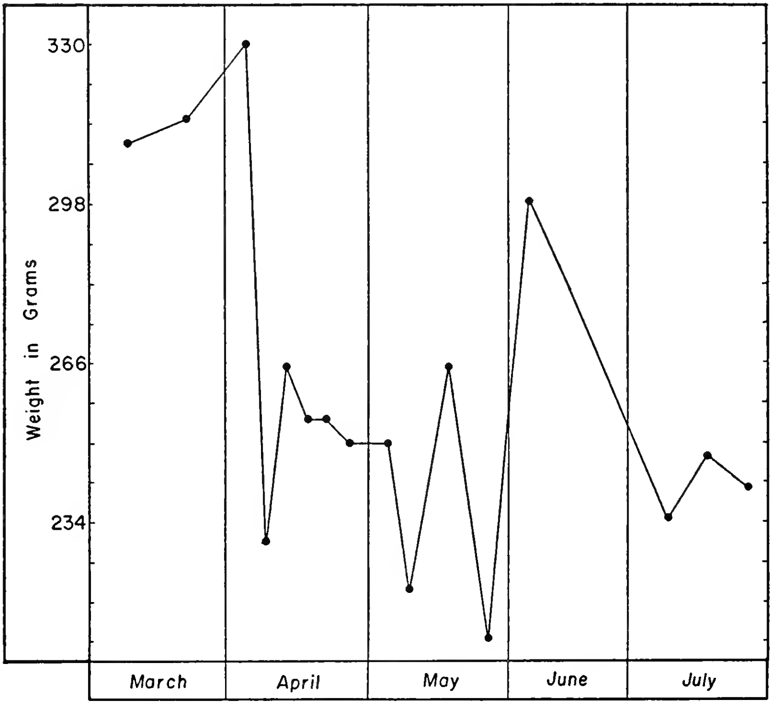


FIG. 4. Weights of an adult female woodrat illustrating pregnancies in early April and June. A litter was born in April and another probably in late June as indicated by losses in weight.

The gestation period is not known for this woodrat. For *N. f. floridana* Pearson (1952:461) reported gestation as probably between 33 and 39 days, while Hamilton (1953:182) thought it to be approximately six weeks. Wood (1935:108) reported gestation for *N. fuscipes macrotis* as being 33 days. Poole (1940:266) suggested 30 or 36 days for *N. magister,* and Richardson (1943:130) thought gestation to be more than 38 days in *N. albigula.*

On May 11, 1952, a female found in a live-trap with an adult male was in breeding condition; a semi-solid, whitish, translucent plug filled her vagina. She was recaptured 33 days later, on June 13. In this interval she had increased in weight from 152 grams to 216 grams. Her abdomen was swollen and foetuses could be detected by palpation. When caught again eight days later her weight had decreased to 180 grams indicating parturition in the intervening period. If this female was successfully bred by the male while they were in the trap together, gestation was more than 33 days and less than 41 days. A similar vaginal plug was recorded in one other female.

Conclusive evidence that females breed in their first season was not obtained. One young female first caught in late May, 1953, weighed 143 grams and was imperforate. When next captured, on August 15, 1953, she was perforate and her weight had increased to 224 grams; possibly she was pregnant. If females attain sexual maturity near the end of the first season they would have to be of early litters, but it seems that ordinarily breeding is delayed until the next season. The records for all females for which reproductive data are available are presented diagrammatically in Figure 5. In most instances the birth of a litter was assumed when the pregnant female underwent a sharp loss in weight and her mammary area took on the characteristic appearance indicating nursing of young. Some females may have absorbed their embryos, but this could not be readily detected. In each of a few instances, the estimated age of young caught with a female was used to estimate the date of birth of the litter. Again incompleteness of individual records prevent yearly comparisons.

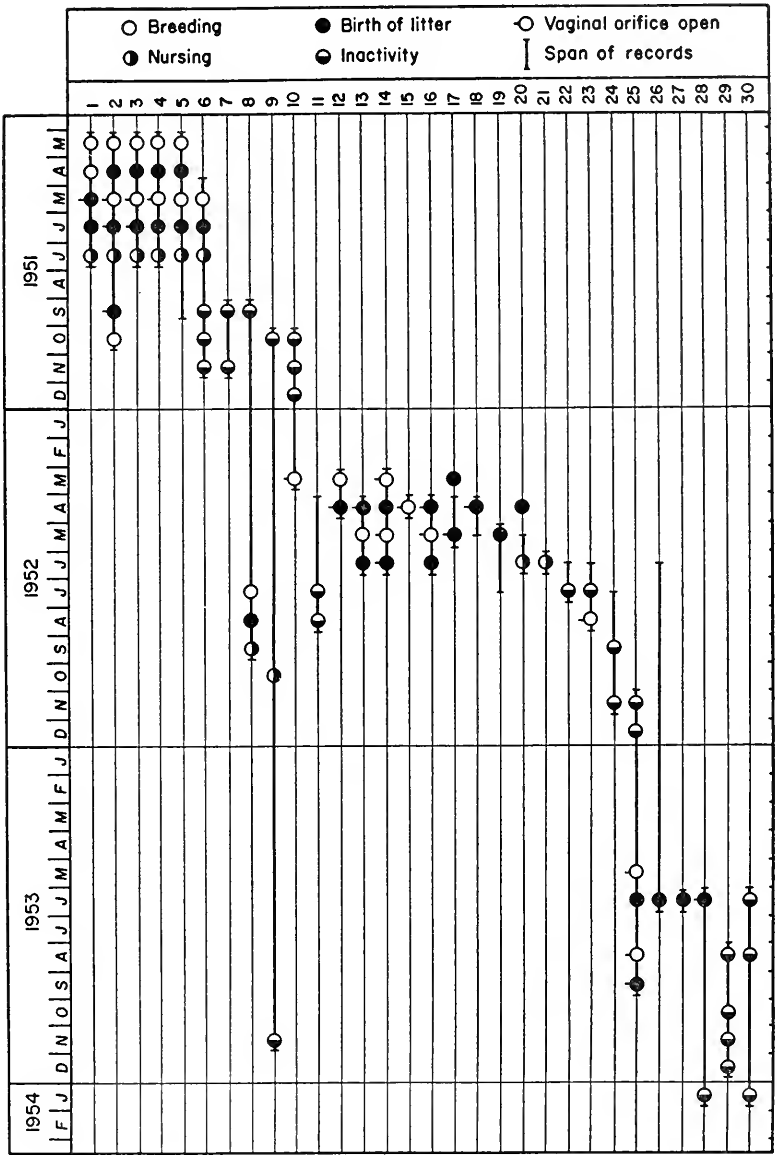
Size and Numbers of Litters

Sizes of litters could rarely be determined with any degree of certainty from live-trapping because the young caught at a house might not represent the entire litter, one or more having been eliminated before weaning. Sometimes it was impossible to determine to which female young belonged, because of the close proximity of several females, especially at the outcrop.

Females have been recorded with from one to five young or embryos. Seemingly, the most common number of young per litter is two. One female was known to have two litters of two each. Another female was seen nursing two young. A female that died in captivity contained two embryos, one in each uterine horn. When litter size could be ascertained with some certainty by live-trapping, two per litter was the most frequent number. One female was found in a stick house with one young. Another female driven from a house in a hedge row had three young attached to the teats. The label on a study skin in the University of Kansas Museum of Natural History records that there were three embryos. Dr. James Findley, told me of a female examined by him which contained four embryos, two in each uterine horn. A female that I dissected had five embryos, one in the right horn and four in the left. Another female bore a litter of five in captivity. For these 13 litters the average number per litter was 2.7. It is unlikely that all members of litters containing as many as five young survive under natural conditions, because the female has only four teats. The female that reared five in captivity probably was successful because she did not have to leave one of the young. The young lacking a teat would not remain without food for any great length of time. Reports in the literature (Table 8) of sizes of litters and averages for several species of woodrats indicate a general similarity throughout the genus. Most samples average between two and three per litter, but in *N. cinerea* the average is higher than three and in *N. albigula* the average is a little less than two. When there was a sufficiently large sample, the most common number per litter was two—a small number compared to that of many species

FIG. 5. Reproductive data and span of records for all female woodrats, on the study area, for which records are available.

Female 1 seemingly had a litter in early May, 1951, and was bred again almost immediately. Female 2 was gaining weight steadily until the last capture, on October 21, 1951, which might have indicated pregnancy. Female 10 was not bred until some time in March, 1952. Female 11 was in a late stage of lactation on July 16, 1952, and she had young probably in June, 1952. Female 12 may not have survived long enough to bear young. Female 15 was in a live-trap with a breeding male on April 12, 1952, but she was found dead in a trap on May 2, 1952. Female 16 was in a live-trap with a breeding male on May 11, 1952. Two young caught at the house of female 17 were estimated to have been born in late March. A litter was born to female 18 in late April, 1952, but she died from heat exposure on May 2, 1952. Female 19 was in a trap with a young male estimated to have been born in May. A young female, estimated to have been born in April, was in a trap with female 20 on June 24, 1952. Female 20 may have been bred again in August. The teats of female 21 indicated she had nursed a litter in June, 1952. Female 23 may have borne a litter in June, 1952. Female 25 may have had a litter in May, 1953; she seemed to be nursing when caught on May 28, 1953. A litter of five was born in captivity to female 27 on June 9, 1953.


○ Breeding
◑ Nursing
● Birth of litter
⊖ Inactivity
-○ Vaginal orifice open
I Span of records
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
1951
M A M J J A S O N D
1952
J F M A M J J A S O N D
1953
J F M A M J J A S O N D
1954
J F

of rodents. Vorhies and Taylor (1940:475) suggested that the low reproductive rate found by them in *N. albigula* resulted from relative freedom from enemies owing to protection by the house, and would apply equally well to other species.

The trapping records of most females were not complete enough to trace individual histories of breeding completely even through one entire season. Neverthless, records of several females show two litters per year, and evidence for the birth of three litters in a season is available for two females, one of which possibly had four litters.

One of these females first caught on March 24, 1951, was pregnant, and she weighed 310 grams on March 28. By April 8, her weight had increased to 315 grams, and she was obviously in a late stage of pregnancy because her abdomen was swollen and foetuses could be detected by palpation. At the next capture six days later, parturition had occurred, with a loss in weight of 100 grams. Possibly this was her second litter of the season, and she became pregnant again sometime in late April or May. By June 3, she weighed 300 grams. The litter was born in early June and she was still nursing by July 1. Seemingly, none of her litter survived because the only young caught near her house was judged to belong to another female.

Another female first caught on March 25, 1951, was pregnant then and bore her litter sometime in April. She was found in a trap with a male in breeding condition on May 11. Seemingly, mating was successful because she had increased in weight to 305 grams by June 3; young were probably born in mid-June.

A female that seemingly had at least three pregnancies in one season was pregnant in March, 1951, when first caught and bore a litter in late April. It is not known whether this was the first or second pregnancy. She became pregnant again in May and bore another litter in June. In later September the appearance of the teats and mammary area indicated that she was then nursing her third litter (or perhaps her fourth if she had borne young in late February or early March). A summary of all young captured in live-traps is included in Table 9. Young that were recorded in other places are included.

The reproductive potential for *N. floridana* is not known precisely, but it is lower than in most other small rodents. Life expectancy for adults is longer than for more prolific species; population turn-over is relatively slow.

TABLE 8. SIZE OF LITTERS AND AVERAGES (OR MODALS) REPORTED IN THE LITERATURE FOR VARIOUS SPECIES OF WOODRATS.

Author	Species	Size	Average	Remarks
Kellogg (1915)	*N. floridana osagensis*	3–6		
Dice (1923)	*N. floridana osagensis*	2		Based on one record
Svihla and Svihla (1933)	*N. floridana rubida*	1–4		3–4 most common
Worth (1950)	*N. floridana floridana*	1–4		2–3 most common
Pearson (1952)	*N. floridana floridana*	2–4		3 of 7 litters with 3
Harper (1927)	*N. floridana floridana*	2		one record
Chamberlain (1928)	*N. floridana floridana*	3		one record
Poole (1940)	*N. magister*		2	10 litters
Vorhies and Taylor (1940)	*N. albigula albigula*		1.95	93 litters
Richardson (1943)	*N. albigula*	2–3		3 as maximum
Warren (1926)	*N. albigula albigula*	1–4		
Warren (1926)	*N. albigula venusta*	2		one record
Warren (1926)	*N. albigula warreni*	2–3		3 records
Feldman (1935)	*N. albigula albigula*		2 Modal	29 litters
English (1923)	*N. fuscipes*		2.8	
Donat (1933)	*N. fuscipes annectens*	2–3		6 litters
Linsdale and Tevis (1951)	*N. fuscipes luciana*	1–4	2 Modal	
Vestal (1938)	*N. fuscipes annectens*	1–4	2.6	
Gander (1929)	*N. fuscipes macrotis*	3		one record
Warren (1926)	*N. fuscipes streatori*	1–2		
Warren (1926)	*N. micropus micropus*	3		one record
Warren (1926)	*N. micropus canescens*	3		one record
Feldman (1935)	*N. micropus canescens*	2		11 litters
Warren (1926)	*N. mexicana fallax*	2–4		
Warren (1926)	*N. lepida lepida*	5		one record
Warren (1926)	*N. cinerea cinerea*	1–4	4	
Warren (1926)	*N. cinerea saxamans*	3–4		3 litters
Warren (1926)	*N. cinerea arizonae*	4–6		3 litters

Parturition

A female in a late stage of pregnancy was live-trapped on June 6, 1953, brought to the author's home and placed in a cage. She was extremely docile and soon accepted food. By June 8, she was consuming twice as much food as any of the other rats in captivity. Most of the time she was listless and lay stretched out on one side or on her venter with the hind legs extended posteriorly. Seeming restless, she frequently shifted positions. Even when eating she was frequently prone on the floor of the cage supported by her elbows. From 4:00 P. M. June 9, until 12:30 A. M., she spent most of the time in an extremely restless sleep with frequent shifts in position. Occasionally she would eat a small amount but would return directly to the cotton nest and sleep again. At intervals of approximately

TABLE 9. SUMMARY OF YOUNG BORN ON STUDY AREA AND RECORDED ELSEWHERE (*). THE ESTIMATED TIME OF CONCEPTION IS BASED ON A GESTATION OF FIVE WEEKS.

Sex	Age in days	First capture	Estimated birth date	Estimated time of conception	Number of captures	Span of records	First weight (gms)	Change in weight
Female	30	June 9, 1951	May 19	April 15	3	24	......	......
Male	59	July 3, 1951	May 5	April 1	8	152	108	192
Male	38	Oct. 14, 1951	Sept. 6	Aug. 2	2	7	77	12
Male	33	Apr. 26, 1952	Mar. 24	Feb. 18	2	2	67	-3
Female	33	Apr. 27, 1952	Mar. 24	Feb. 18	9	106	63	77
Male	33	May 8, 1952	April 5	Mar. 2	12	392	64	159
Male	48	June 13, 1952	May 6	April 2	1	0	71	0
Male	60	June 18, 1952	April 19	Mar. 9	5	8	103	-4
Female	60	June 18, 1952	April 19	Mar. 9	5	351	90	106
Male	28	June 19, 1952	May 22	April 18	1	0	51	0
Male	45	June 19, 1952	May 5	April 1	3	23	80	15
Female	69	June 19, 1952	April 11	Mar. 7	2	5	114	0
Female	45	June 20, 1952	May 5	April 1	9	83	96	64
Male	84	June 21, 1952	Mar. 29	Feb. 23	1	0	130	0
Female	94	June 22, 1952	Mar. 20	Feb. 14	1	0	140	0
Male	59	June 26, 1952	April 28	Mar. 25	2	2	104	2
Male	99	July 15, 1952	April 7	Mar. 4	24	243	156	98
Male	64	Aug. 11, 1952	June 8	May 5	1	0	112	0
Female	89	Sept. 12, 1952	June 15	May 12	2	149	136	13
Female	?	May 28, 1953	?	?	8	79	143	81
Female	63	June 3, 1953	April 1	Feb. 25	8	13	113	3
Female	69	June 4, 1953	Mar. 27	Feb. 21	1	0	116	0
Female	44	June 5, 1953	April 22	Mar. 19	6	9	83	0
Male	44	June 5, 1953	April 22	Mar. 19	1	0	94	0
Female	69	June 5, 1953	Mar. 28	Feb. 22	10	216	119	72
*Female	50	Nov. 10, 1953	Sept. 21	Aug. 18	......	......	98	......
*Male	29	May 16, 1954	April 17	Mar. 14	......	......	61	......
*Male	19	Mar. 28, 1954	Mar. 9	Feb. 3	......	......	42	......
*Female	19	Mar. 28, 1954	Mar. 9	Feb. 3	......	......	44	......

three to four minutes, movement of the foetuses would cause a bulge to appear in the abdominal region. The instant preceding this movement by the young, the rear legs of the female would suddenly retract. Perhaps this was a sign of pain. The interval between movements of the young became progressively shorter. The vaginal orifice was observed to be open. Observations were terminated at 12:30 A. M., on June 9, and when resumed at 7:00 A. M., four young had been born, and all were attached to nipples. The female was giving birth to a fifth at 7:05 A. M. She was in an upright position with all feet on the floor of the cage. The female remained for 10 minutes in an upright position, bent with the head between the rear legs, and began chewing and licking. She turned permitting a view of the newly born young and appeared to bite off the attached piece of umbilical cord. For two hours following birth, the last young remained uncleaned and unattached.

Newborn young

The newborn woodrats were slate gray on the back, about halfway down the sides and on the head, except for the tip of the muzzle, which was pinkish. Scattered light-colored hairs over the back were visible only under magnification. The underparts were pale owing to a sparse covering of white hairs. The dorsal part of the tail was dark near the base with pigmentation decreasing in intensity toward the distal end. The tail was wrinkled so that it appeared segmented. The pinnae were folded downward over the external auditory meatus. The vibrissae were four to five millimeters long. The eyes were closed. Claws were evident but small. Both upper and lower incisors had erupted. Hamilton (1952:186) has described and pictured incisors of newborn young of *N. f. floridana* and discussed their adaptation for attachment to the nipples. Young are capable of moving slowly by actively wriggling almost as soon as born. Hamilton (*loc. cit.*) states: "Sex is readily determined at birth, the four mammae being evident in the young females." This was not observed by me.

Care of young

Females nursing young frequently leave the house when disturbed, to seek refuge in a tree with the young attached to the teats. Young that are near weaning have not been observed to cling thus to the teats and the mother abandons them. Females in captivity will hover over the young protectively but will not actively defend them, and upon provocation will leave them if they are unattached. When young left in the nest while the mother was in another part of the cage were caused to squeal the mother would not return to them but would retreat to one corner. As soon as the disturbance ceased, she would return to the young.

The female that bore and reared the litter in captivity spent most of her time in the first month nursing the young. In nursing, she most frequently lay on her side. At times she would lie on her abdomen with the posterior part of the body elevated allowing space for the young to suckle. She frequently cleaned them by licking, turning them with her front feet. On the second day after birth the mother was observed to remove them from the teats by pushing on their shoulders or hips. After the young were older (18 days) she would dislodge them by turning in a small circle pushing with both front feet and her nose. Several rotations were required to loosen all five young. Because the four teats did not accommodate all the young, one, not always the same individual, was attached to the clitoris which soon became greatly enlarged probably from irritation by the suckling young. The mother rotated the young allowing all to feed. The mother was never observed to display irritation toward the young for the period that they were together.

Development and Growth

The five young (three males, two females) averaged 10.4 grams in weight two hours after birth. The largest weighed 11 grams and the smallest 9.8 grams. They averaged 87.4 millimeters in total length. Hamilton (1953:183) recorded average total length for 21 newborn *N. f. floridana* as 93 millimeters and average weight as 14 grams.

The pinnae of all young unfolded and erected the second day, although the external auditory meatus remained closed. Also by the second day, the dorsum was almost black. The underparts were reddish. The young characteristically held their tails elevated in an arc. When they lay sleeping unattached to a nipple, they twitched, causing the entire body to move, at intervals of 20 to 45 seconds. A similar jerking motion was observed when they were attached to teats but was limited to the hind legs.

On the fourth day, the dorsum, head, and outer surface of the legs had a uniform covering of short black hair. There were also longer, light gray hairs scattered on the back. The abdominal region had short white hairs visible only with magnification. The inside of the pinnae had a sparse covering of short, straight gray hairs. The external auditory canal had not opened. The eyes, still closed, protruded more than at birth. The incisors were unchanged and almost translucent under a dissecting microscope. The posterior pads of the rear feet had acquired a light gray tinge. Even by this time, nipples were not evident. The young made a wheezing sound in breathing when they were not attached to a nipple. As much time as the mother would allow was spent in nursing. While the young were still attached, the mother frequently cleaned them by vigorously licking them. She usually licked the anal region more gently. The young attached so firmly to the nipples that they could be removed only by exerting a firm, steady pull and twisting them. When the young were replaced with the mother, they squealed loudly and actively squirmed to find a nipple.

On the eighth day the young that was attached to the clitoris was extremely difficult to remove, and the clitoris was lacerated by both upper and lower incisors. By this date the fur had thickened considerably. The vibrissae were approximately 10 millimeters long and when they were touched the young folded them along-side the head. The hair on the abdomen was also thicker. The tails were distinctly bicolor with short black hairs on the upper surface and white hairs on the lower surface. The wrinkles were not as evident as they had been at birth. The soles of the hind feet were deeply pigmented while no pigmentation was visible on the front feet. Hairs on the inner surface of the pinnae were more numerous and longer; the external auditory meatus was still closed. The upper incisors were approximately half the length of the lower. The area around the vibrissae was not so pinkish as earlier. The young were capable of active movement but had difficulty in forward progression. The eyes had increased in size and appeared to be closed as if sleeping. The wheeze when breathing was accompanied by an audible squeak.

By the fifteenth day, the eyes of all the young had opened. As far as could be determined while they were attached, the eyes had not completely opened the previous day. The young were able to run with well-coordinated movements, and spent more time unattached foraging about the cage. The incisors were almost together but the lower incisors were still about twice as long as the upper. The hair on the ears had increased in length. The dorsum appeared more gray but was still darker than the sides. This dark hair was prominent on the outer surface of the legs down to the wrist and the ankle. The region around the vibrissae had lost the pink color. The young urinated copiously and the feces were still formless and light brown.

On the sixteenth day, one young was observed attempting to eat a sunflower seed. However, it was unable to break through the seed coat. The young were able to clean and scratch themselves. Later the same day, one was observed eating lettuce. The food was held in the front teeth in the characteristic adult fashion. On the following day, one young woodrat exhibited aggressiveness in biting the finger of the person handling it.

By the twentieth day all the young took solid food even though they still nursed. They were able to climb the sides of the cage. Except for increasing size, no significant change had taken place.

At six weeks of age (average weight, 86.4 grams) they still occasionally attached to the nipples although the size of the nipples indicated lactation had stopped. One was observed attached when

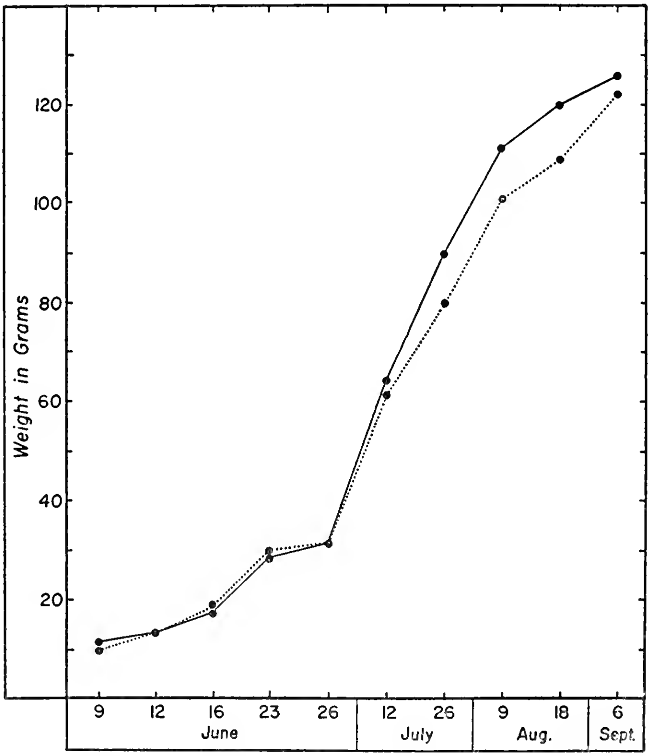


FIG. 6. Weights of a litter of five young (three males and two females) born and raised in captivity. The solid line represents average weights of the males; the broken line indicates average weights for the females.

it was ten weeks old but under natural conditions suckling probably is discontinued earlier.

Woodrats increase rapidly in weight from birth to approximately three months of age (Figure 6), thereafter the rate of increase slackens and full adult weight usually is not attained until the animal reaches an age of eight months or more. However, individuals occasionally undergo extremely rapid growth and reach adult size in a much shorter time. One male woodrat that weighed 108 grams when first caught on July 3, 1951, was estimated to have been born in early May. He was last captured 152 days later on December 2, 1951. By then his weight was 300 grams, an increase of 1.2 grams per day on the average, to a size near the maximum. Figure 7 illustrates the comparison between the growth of this male and another young male that required a considerably longer time to reach adult size. The latter male first captured on July 15, 1952, and weighing 152 grams, was estimated to have been born in late

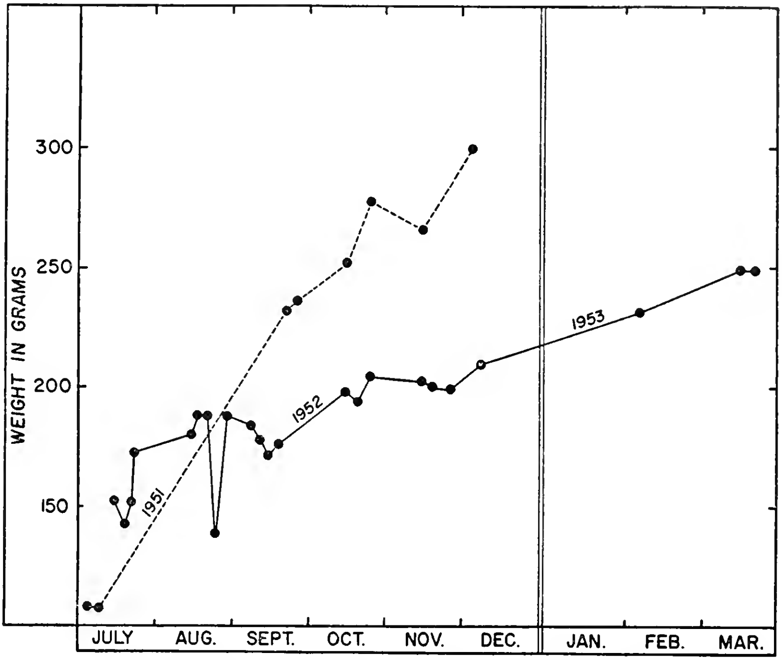


FIG. 7. Differences in growth of two young males. The male represented by the broken line was born in 1951 (probably in May) and lived only until the following December. The second male (solid line) was born in 1952 and was last caught on March 15, 1953.

March or early April. He was last caught on March 15, 1953 (243 days), and weighed 250 grams having gained 98 grams, an average daily increase of only .4 grams. Figure 8 illustrates still another instance in which growth was perhaps even more retarded. This male was first caught on May 8, 1952, and weighed 64 grams. When last captured 392 days later the weight had increased 159 grams; this also was an average daily increase of .4 grams. However, the weight of 223 grams at last capture when more than a year old was still less than that of most adult males. Females tend to lag slightly behind males in weight gains. Possibly drought in 1952 and 1953 retarded growth.

Survival of Young

Of 27 young (average weight 103.4 grams) captured on the study area, six were caught only one time. The average span of records for the young caught more than one time was 25.5 days. Of the six that were known to have reached adult size, three seemingly did not survive long enough to breed. So far as known, of the 27 young only 11.1 per cent survived to contribute to maintenance of the local population. A young male first caught on

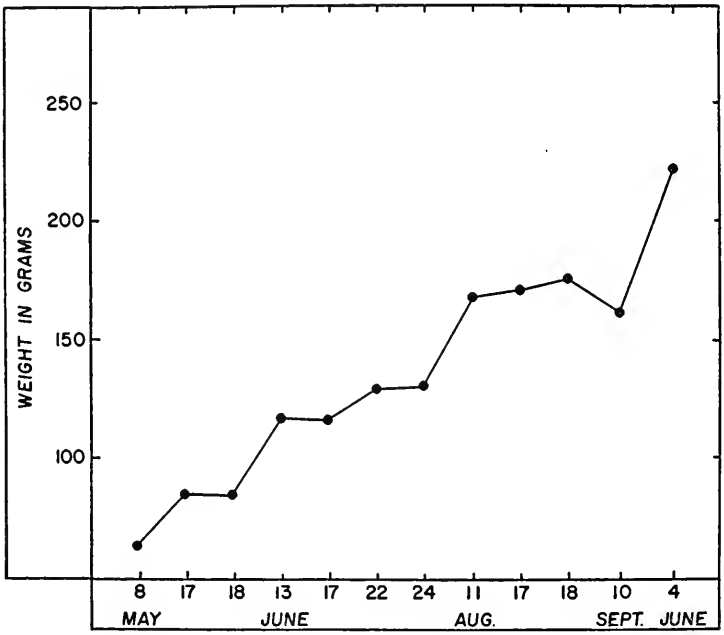


FIG. 8. Growth of a young male born in 1952 (probably in April) that survived to sexual maturity. He was last captured on June 4, 1953.

July 15, 1952, was last seen 243 days later on March 15, 1953; another male survived 392 days and a female survived 331 days and bore at least one litter of young. None of the young live-trapped along the western section of outcrop were known to have survived to sexual maturity.

The minimum number of young that should have been produced from known pregnancies greatly exceeded the number caught in traps. Most of those unaccounted for probably did not survive until weaning. Perhaps resorption of embryos is also an important factor.

The poor survival of young after weaning may be partly explained by their inability to establish new houses owing to scarcity of building sites. This would be more pronounced in the woodland section where the brush heaps were limited. Young are probably more susceptible to natural enemies than adults. Small to medium sized snakes that would be unable to capture and overcome adults could take young rats. Some of the young possibly perished while the mother was in a live-trap over night for periods up to 12 to 14 hours. Extremely young rats might be killed from exposure especially in cold weather in March.

CHANGES IN PELAGE

The pelage of woodrats approximately one month old has a faint brown wash that is more noticeable on the cheeks. The first molt begins when young are five to six weeks old. The molt starts on the abdomen, chest, and throat and progresses dorsally. The new brown hair is usually first discernible on the outer sides of the front legs and also on the cheeks. The growth of new hair progresses more rapidly ventrodorsally on the middle of the body. However, new brown hair usually is observed on the hips before the molt reaches the mid-dorsal line. After reaching that line the molt progresses more slowly anteriorly and posteriorly. A narrow band of new hair grows posteriorly on the sides of the head passing behind the ears to meet in the mid-line between the ears. New hair grows back over the forehead to meet that coming in behind the ears. The molt ends in a small zone across the back about midway on the body leaving an anterior region and a posterior region. Just previous to this stage the triangular anterior area connects to the part on the rump by a narrow band down the back. After separation, the anterior region is triangular; the widest part is across the shoulders. The point of the triangle extends down the mid-dorsal line. The posterior region lies across the rump. In some individuals the rump is the last area to molt whereas in other individuals the last to molt is a small spot between the shoulders. The brown color of new hair after this molt has been completed is not so intense as in adult pelage. Generally, it also lacks the Pinkish-Cinnamon color especially along the lateral line.

The time and rate at which the rat first molts varies with individuals as well as with size and age. One young male of 103 grams first caught on June 18, 1952, had new brown hair visible on the face, sides of front legs, and flanks. In addition, there was new brown hair on the rump and upper parts of the hips which could be seen only by parting the old gray hair. Eight days later, the first molt was considered to be complete. A young female of 90 grams caught the same day was in a later stage of molt but completed it about the same time as the male. New brown hair was visible without parting the old fur on the flanks and arms. However, by parting the old hair new brown hair could be seen over the back and rump. Ten days later she had completed this initial molt. Another young female (63 grams) seemed not to be molting when first caught on April 27, 1952. However, three days later new brown fur could be seen by parting the old fur on the sides and back but not on the rump. Possibly the molt was in progress when she was first captured, but it was overlooked owing to difficulty of detecting new hair on the abdomen. By May 8, 1952, new hair was observed close to the skin on the rump. Brown hair was visible on the face, flanks, and behind the ears. Two days later the over-all appearance of the dorsal pelage was dusky, washed with a brown tinge. By May 16, the only gray left was between the shoulders. At this date her weight was 109 grams. Another male (64 grams) was in about the same stage of molt on May 8, 1952, as the above female when she was first caught. When next caught on June 13, 1952, the first molt was recorded as complete. He then weighed 118 grams.

The pattern of the second molt which immediately follows the initial molt is not so well known owing to inadequate records of individuals. Linsdale and Tevis (1951:455-456) described a second molt from "immature" to "subadult" pelage for the dusky-footed woodrat. The initial molt of *floridana* described herein agrees closely with the initial molt (juvenal to immature) described by Linsdale and Tevis for *N. fuscipes*. However, I was unable to establish a pattern in the second molt that agrees with the similar stage described by them. They described the second molt as starting on the rump and progressing uniformly forward. A male under observation from July 15 to 31, 1952 acquired no new hair, but gained in weight from 152 to 172 grams. New hair was observed on the flanks at the "lateral line" from August 15 (181 grams), until August 21. When next caught on September 6, the new hair was showing through on the flanks and new younger hair was observed over the thighs. By September 12 (177 grams) new hair was visible on the front legs, flanks, anterior one-half of the thighs, and behind the ears, and could be seen on the rump by parting the old pelage. On the basis of this rat's size when first caught this molt was thought to be his second, and the pattern was similar to that of the initial molt. One month later when this male weighed 198 grams, he was molting in patches; probably this was the third molt preceding attainment of adult pelage.

A young female first caught on August 16, 1953, weighed 150 grams and was in molt, judged to be her second, on September 9, 1953. There was new hair close to the skin on the mid-dorsal line, up to the shoulders and for a short distance on either side of the mid-line. New hair was visible at the "lateral line" without parting the old fur and obviously represented older hair than on the back. No new hair was observed on the rump. Progression of the molt seemed to be principally from the ventral to the dorsal surface.

The next change in pelage, which occurs in patches with no regular pattern, results in acquisition of the adult pelage. Seasonal molts of adults also occur in patches. When old adults undergo a molt, the worn pelage sheds readily especially when the animal is handled. In several instances, patches of new hair were still close to the skin but the old hair had already fallen. This rapid shedding of old hair while new hair is short results in a ragged appearance.

MOVEMENTS

Home range, territoriality, shifts from normal foraging range, dispersal of young, longevity, and some related matters are treated in another paper by Fitch and Rainey (1956:499-533).

POPULATIONS

Numbers and Ratios on Study Area

In the period from March 24, 1951, to June 24, 1954, 105 woodrats were live-trapped 660 times on the area of study. The woodrats were not abundant at the beginning and they decreased in numbers throughout the period of study. In February, 1955, one night of sampling did not yield any captures. The population in the woodland section was completely eradicated as a result of burning of most of the houses by the landowner. Two houses at the eastern section of the outcrop with long histories of occupancy were dismantled in February, 1955, and found to be abandoned. Most of the live-trapping was done in 1951 and 1952. Table 10 summarizes total trap nights for the three areas for the four years. Table 11 summarizes trapping records for the years 1951, 1952, and 1953. Table 12 illustrates higher mortality in June than other months involving chiefly the young. Trapping was not continuous. It is believed that live-trapping, especially when carried on for several succeeding nights, results in the capture of most individuals present in the area, but some few exceptionally wary individuals may not enter traps. From the data obtained, numbers present each month and annual trends can be demonstrated with a fairly high degree of accuracy.

Of the 105 woodrats live-trapped, 47 (44.7 percent) were females and 58 (55.3 percent) were males. Females were caught 362 times and males were caught 298 times. This difference results from males tending to wander more than females. Females tend to be caught repeatedly at one house. The difference in sex ratio is not considered to be significant. Yearly sex ratios including only newly marked rats are: 1951, 17 males and 11 females; 1952, 28 males and 25 females; and 1953, six males and 11 females.

TABLE 10. SUMMARY OF TRAP-NIGHTS FOR THE THREE AREAS OF THE TRACT STUDIED.

Section	1951	1952	1953	1954	Totals
Eastern area	823	592	317	70	1,802
Western area	....	150	120	42	312
Woodland	....	566	58	4	628
Totals	823	1,308	495	116	2,742

On the basis of pelage color, weight, general body proportions, and in some instances, time of year when first captured, woodrats were classified in three age groups: juveniles, subadults, and adults. Even though three molts were detected from young to adult, this feature could not be used to distinguish a fourth age group as was done by Linsdale and Tevis (1951:450) for *N. fuscipes.* In this report, subadults are considered to undergo one molt before attaining adult pelage.

Woodrats were recognized as being juveniles until they completed their first molt. The gray juvenal pelage is easy to recognize because it contrasts with any new brown hair which might be present. Generally, weights were less than 150 grams although some individuals weighed more when they completed the first molt. On the other hand, some females weighing approximately 145 grams were diagnosed as subadults.

The brown of subadult pelage is not so intense as in adult pelage. Subadult pelage lacks the Pinkish-Cinnamon color along the "lateral line" which is usually prominent in adults. Adults are more robust and muscular than subadults. The skin of subadults fits loosely and is thinner. Subadult males weigh from 170 to approximately 250 grams and subadult females from approximately 150 to 200 grams. Subadults first caught in autumn or early winter usually were young adults by the following February or March. Rats were classed as adults when they showed first external signs of sexual maturity. Others first caught in nonbreeding season were called adults because of size, weight, and color of pelage. It could be safely as-

TABLE 11. SUMMARY OF TRAPPING RECORDS FOR THE ENTIRE STUDY AREA, FOR 1951, 1952, 1953.

Date	New individuals						Previously marked		Total captures	Total trap nights
	Males			Females			Males	Females		
	J*	SA**	A***	J	SA	A				
1951										
Mar.	......	......	3	......	......	5	......	......	13	71
April	......	......	3	......	......	1	1	5	31	182
May	......	......	2	......	......	......	4	6	66	180
June	......	......	......	1	......	......	6	6	33	100
July	1	......	......	......	......	......	3	7	30	140
Aug.	......	......	......	......	......	......	......	......	......	......
Sept.	......	2	......	......	2	......	3	3	15	40
Oct.	1	2	1	......	......	2	2	2	16	44
Nov.	......	......	1	......	......	......	5	1	7	22
Dec.	......	......	1	......	......	......	6	......	9	44
Totals	2	4	11	1	2	8	......	......	220	823
1952										
Jan.	......	......	......	......	......	......	5	1	10	110
Feb.	......	1	......	......	......	......	3	2	14	132
Mar.	......	......	4	......	1	4	......	2	15	95
April	1	......	4	1	......	3	3	4	42	90
May	1	......	1	......	......	1	2	7	41	140
June	6	......	1	4	......	6	3	5	59	237
July	1	1	1	1	1	1	2	6	39	135
Aug.	1	2	3	......	......	......	7	7	43	190
Sept.	......	......	......	......	1	......	4	4	15	137
Oct.	......	......	......	......	......	......	4	1	13	40
Nov.	......	1	......	......	1	......	3	1	14	28
Dec.	......	......	......	......	......	......	2	1	4	14
Totals	10	5	14	6	4	15	......	......	309	1,308
1953										
Jan.	......	......	......	......	......	......	......	......	......	......
Feb.	......	......	......	......	......	......	2	1	3	14
Mar.	......	......	......	......	......	......	2	......	3	44
April	......	......	......	......	......	......	......	......	......	......
May	......	......	1	1	......	......	1	1	6	35
June	2	......	......	4	......	3	5	3	62	247
July	......	......	......	......	......	......	......	......	......	......
Aug.	......	......	......	......	2	......	1	3	6	34
Sept.	......	1	1	......	1	......	1	2	13	49
Oct.	......	......	......	......	......	......	......	......	......	......
Nov.	......	......	......	......	......	......	1	2	9	60
Dec.	......	......	......	......	......	......	1	1	4	12
Totals	2	1	2	5	3	3	......	......	106	495

* Juvenile   ** Subadult   *** Adult

TABLE 12. DISAPPEARANCE OF WOODRATS BY MONTHS. RECORDS FOR JUNE, 1954, NOT INCLUDED BECAUSE FIELD OPERATIONS WERE TERMINATED THAT MONTH.

Date	1951	1952	1953	1954	Totals	Per cent
January		3	1	2	6	6.3
February		3			3	3.2
March	2	1	2		5	5.3
April		7			7	7.4
May		3	1		4	4.2
June	2	15	10		27	28.4
July	6	5			11	11.5
August		7	3		10	10.5
September	2	4	3		9	9.5
October	2	1			3	3.2
November	2	3	1		6	6.3
December	3		1		4	4.2

sumed that they were sexually mature. In one young subadult male unusually early enlargement of the testes to 5 millimeters occurred in his first summer when he weighed 171 grams, but the testes did not descend into the scrotum and he was not considered to be fertile. In general, woodrats mature sexually somewhat before they show other morphological traits characteristic of adults.

Population Trends

When live-trapping was begun in March, 1951, and for the remainder of the year, trap sites were only at the eastern section of the outcrop. In the latter part of March, 1952, live-trapping was begun in the woodland. Several traps were moved to the western section in June, 1952. Because of the small numbers involved, population trends were partly obscured by such factors as trap-raiding and deaths in traps from heat prostration. However, it was obvious that the woodrats were not able to recover sufficiently to replace losses. Figure 9 illustrates increasing difficulty in live-trapping woodrats by 1953 owing to low numbers.

The populations at the western section of outcrop and at the houses in the nearby woodland were considered separately for purposes of convenience. However, especially among the males, there was probably more interpopulation flow than the records show. The permanent occupants of the houses in the woodland and at the outcrop were mostly females. In the breeding season it seemed that most males were wandering in search of females. Of the 23 rats caught at the western section of outcrop, only four were adult males and three of these had moved up from the woodland houses.

The disappearance of adult males may have been correlated with movements between the outcrop and the woodland houses. Such trips were hazardous because there were no available routes having abundant overhead cover. Trees were almost the only places of refuge in time of danger.

In the spring of 1951, the colony of woodrats at the eastern section of outcrop was probably not at its peak, but population density remained greater there than in most other areas (Figure 10). There were from 10 to 12 adults present and all appeared to be in good health. Most of the females were recorded as being pregnant. However, there was a conspicuous absence of first-litter young. As previously mentioned they may have died of exposure while the mothers were in traps. March was cool, the average temperature at Lawrence being 4.3° Fahrenheit less than average. Of the 19 rats that were adults when first caught in 1951, 14 (64.3 per cent) did not survive into 1952. Three of the six subadults that moved into the area did not survive until 1952, and only one of the three

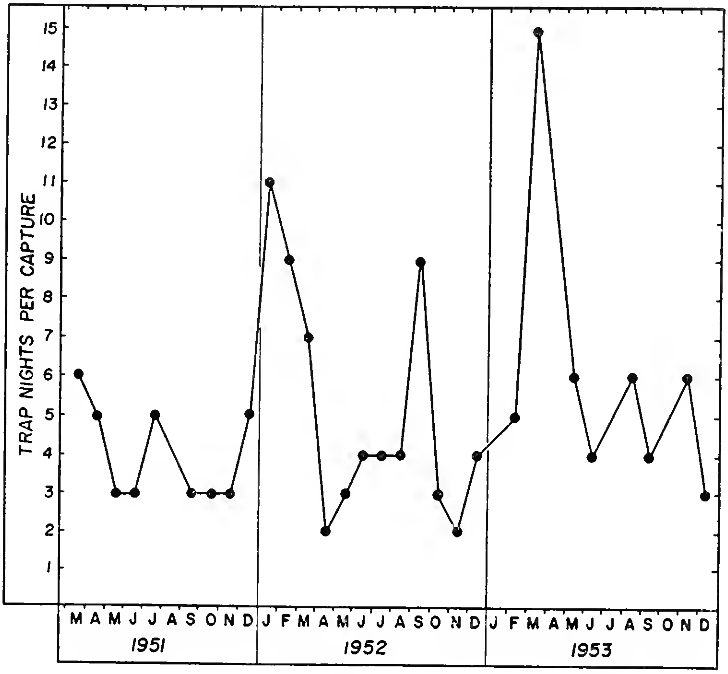


FIG. 9. Number of trap-nights required for each capture for each month that live-trapping was done on the study area.

subadults that survived reached sexual maturity. Excess moisture in June and July at the time when many young were beginning to disperse may have eliminated many. Precipitation at Lawrence was 6.98 inches above average for June and 10.37 inches above average for July. Newly weaned young may be more susceptible to extremes of moisture than are adults.

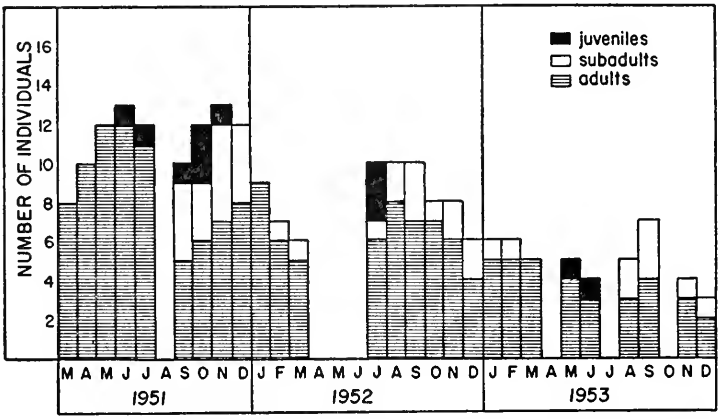


FIG. 10. Trends in the population of woodrats at the eastern section of outcrop in 1951, 1952, and 1953. Diagram based on live-trapping records.

There were only three females and six males present at the beginning of 1952. One of the females was too young to breed in February and disappeared in March and another female left the area, so that only one breeding female remained and five of the six males likewise disappeared before the start of the breeding season. In March, 1952, results from live-trapping at the eastern section of outcrop were so poor (Figure 11) that operations were halted there, and in April, May and June, trapping was done in the woodland instead. In the summer of 1952, the population at the eastern section was increased slightly by immigrants and juveniles. In early autumn of 1952, the population remained stable, but several rats disappeared in late autumn, and by December, there were only three females and three males living at the outcrop. One female disappeared before breeding the next season (February, 1953), two left the area, and were not captured again until May 28, 1953, and November, 1953, respectively. In 1952, the failure of the young to survive was notable, as only one, a young female attained adult size. Of the 22 individuals caught in 1952, 73 per cent did not survive into 1953. Unusual weather may have caused heavy mortality in young and may even have caused losses among the adults. June, which usually has more precipitation than any other month of the year, was the second driest on record for the state.

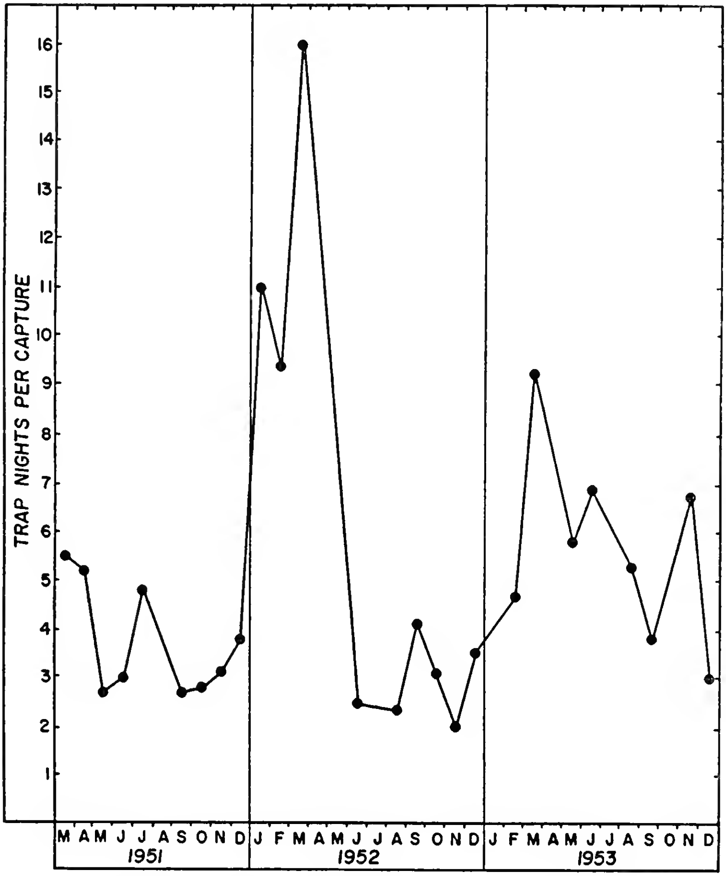


FIG. 11. Number of trap-nights required for each capture for each month that live-trapping was done on the eastern section of outcrop of the study area.

The downward trend continued through 1953, another year of drought. In March, 1953, no females were caught, but two that had been previously marked probably were present as they were recaptured subsequently. The only juvenile recorded was caught in May and it did not survive to adulthood. The population was increased in September by the immigration of one new adult and two new subadults. However, neither of the latter survived. None of the females caught in 1953 survived into 1954.

The population of woodrats inhabiting the eleven houses in the woodland underwent an even more disastrous decline in 1952 (Figure 12). Eventually this population disappeared completely and most of the houses were destroyed by the landowner. When trapping of this population was begun on March 30, 1952, there was a well-established, stable population of at least 15 breeding adults (eight females and seven males). There must have been keen competition for houses because as soon as a house was vacated by one rat, another would move in. Successful breeding in February or March, was indicated by the capture of two juveniles in April, neither of which survived to sexual maturity. Of the 14 adults caught in April, six (five of them males) were not caught the following month. One of these died in a trap. In May, three adult females were lost; two died in traps and the third presumably was taken by a predator.

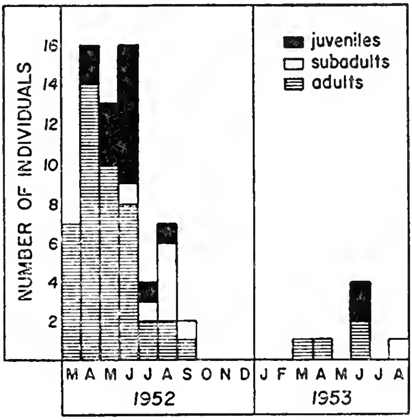


FIG. 12. Trends in the population of woodrats at the woodland section of the study area in 1952 and 1953.. Diagram based on live-trapping records.

The population was greatly decreased in June and loss was especially heavy among juveniles; five of the seven caught disappeared during the month. Also, five more adult females either left the area or were captured by enemies. Young may have succumbed to the unusually high temperatures in this relatively exposed habitat. The temperature at Lawrence was 8.4 degrees above average. The highest reading of the year (105° F.) was in June. For the state as a whole it was the warmest June on record. Vegetation was harmed and there were many consecutive nights without dew. Precipitation was 3.82 inches less than average. Trap disturbances by predators increased in June and by late July results of trapping were not worth the expenditure of effort. Operations were discontinued on July 12. In August the population was increased by the appearance of two subadults but both disappeared in the same month. Thus, of 28 rats caught in the woodland houses in 1952, only three survived into 1953, and they left the area. Two were captured for the last time at the western section of outcrop and the third, a female, returned to bear young in 1953. The loss of 89.3 per cent of the population in less than a year is much too great for a rodent with a relatively low reproductive potential to overcome.

In June, 1953, two adults, male and female, and two juveniles were captured, but only the adult female was caught after June. After she disappeared in August all the houses were abandoned and trapping operations were terminated.

Five adult females and five juveniles (two males and three females) were caught at the western section of outcrop in June, 1952, when trapping was begun there. There was no trap disturbance, but by the end of August, four of the adult females and four juveniles had disappeared. In three nights of live-trapping in September only two individuals were living at this part of the outcrop—a previously marked adult female and a subadult female first caught in June as a juvenile. In the summer of 1953, seven woodrats, all new (three adult females and four juveniles), were living at the outcrop. However, in autumn only two individuals remained—an old subadult female and a new subadult female.

DISCUSSION

Factors Affecting Populations

In the area of my study, for at least eight years prior to 1949, the climatic pattern was good for woodrats. According to reports of competent observers, woodrats were numerous in every habitat type especially on wooded hillsides and hilltops in 1947 and early 1948. At present (1955) they are rarely found in these situations. Evidence of decimating losses in March of 1948 and January of 1949 coinciding with extremes of low temperature with ice and snow storms, have been reported in a separate paper (Fitch and Rainey, 1956:506, 507).

Most small-mammal populations rapidly increase after such disasters, but factors which are not readily detectable have prevented an increase in woodrats. The reproductive potential of the woodrat is relatively low and it would take a longer period of time than would a more prolific species to regain peak abundance. If the number of breeding females is depleted, the recovery period is much prolonged. Even under optimum conditions it almost certainly would take more than one year for the rats to repopulate less favorable areas. In 1951, heavy rains at the time young were beginning to disperse and drought in 1952 and 1953 would perhaps retard to a certain extent reinvasion of the depopulated areas. Extensive destruction or disturbance of hedge rows in the area of study, by man, likewise has resulted in deterioration of habitat and has tended to retard spread into less favorable areas which were formerly occupied. When numbers are exceptionally low, especially in species that live in small colonies, important natural enemies perhaps could prevent a rapid build-up. Both sexes tend to roam more when numbers are low and vulnerability to predators would increase. In this area which is near the northeastern limits of the range of the eastern woodrat, optimum habitat is not so abundant as it is nearer the center of the range. When numbers are low, the ability of rats to repopulate their habitat is greatly reduced because of discontinuity of habitat. If a population is reduced or destroyed in suboptimum situations at the center of the range, re-establishment in these situations would take place faster because of proximity of unaffected populations in optimum habitats.

The number of woodrats in a colony in this area is ordinarily stabilized and the welfare of the colony is strongly dependent on the survival or replacement of productive females. In 1952, juveniles were numerous at the woodland houses and western section of outcrop, but they were scarce at the eastern section of outcrop since this section lacked breeding females. For the population to hold its own, young must be produced at a rate at least equal to the rate at which adults disappear. An example of stabilized conditions and the disastrous consequences involved in their alteration was observed in the colony of rats living in the hedge row described earlier (page 566). Five rats were caught in snap traps at five houses on November 11, 1953. All except one of the remaining seven houses had indications of being occupied. Four of the five houses from which rats were caught were completely dismantled in November and December, 1953. When the area was revisited in early 1955, none of the remaining houses was occupied, and all appeared to have been deserted at least since the autumn of 1954. There was no stored food in any of the houses.

Distributional Patterns and Factors Limiting Dispersal of Populations

Wooded stream courses, and rock outcrops either associated with stream courses or away from them seem to provide the chief dispersal routes for woodrats in Kansas. Hedge rows are important in eastern Kansas but are not present in western Kansas. In Cook

County, Texas, Bailey (1905:109) found *osagensis* in wooded ravines and Russell (1953:461) found it inhabiting dense growths of low shrubs along intermittent streams in the same area. In Oklahoma this woodrat is generally associated with rocky bluffs and wooded, rocky ravines and also occurs in the oak-elm flood-plain forests in the eastern part of the state (Blair, 1939:124). McCarley (1952:108) found it common in the postoak-blackjack and flood-plain forest association in Byron County, Oklahoma. In the vicinity of Stillwater, Payne County, Oklahoma, Murphy (1952:205) reported that *osagensis* preferred the postoak-blackjack ravine situations. Black (1936:33) found it along cliffs and in caves of northwestern Arkansas. In south-central Missouri, Moore (1938:503) observed it inhabiting water-worn cavities in limestone bluffs bordering streams. Also in south-central Missouri, Leopold and Hall (1945:145) observed that *osagensis* lived in crevices in a limestone cliff and in uninhabited buildings.

The Osage Cuestas (Schoewe, 1949:282) are prominent physiographical features of eastern Kansas south of the Kansas River. According to Schoewe (*loc. cit.*) the cuestas ". . . consist of a series of northeast-southwest irregularly trending east-facing escarpments between which are flat to gently rolling plains." The tops of these escarpments are capped by a stratum of limestone and when not covered by deposited soil the edge of the stratum is exposed forming an outcrop. Major streams tend to flow transverse to the escarpment and tributaries tend to follow the vales in between. Erosional action of these streams cutting through bedrock produces rocky ledges along the banks which serve as habitat for woodrats. Kellogg (1915:185) in writing of this woodrat in southeastern Kansas reported that it inhabited cliffs and rocky ledges along streams. He further states: "Old settlers in Labette and Cherokee counties informed me that during the seventies, wood rats were plentiful among the rocks and sandstone ledges near streams." Streams in the Flint Hills have cut deep channels lined with outcropping rock ledges. These and the thicket-covered banks provide requirements for woodrat habitat.

In an early report, Knox (1875:21) stated that woodrats (*N. f. campestris*) were common along the streams of middle and western Kansas. Kellogg (1915:183) recorded woodrats in northwestern Kansas as living along chalk and sandstone ledges. Hibbard (1933:80) reported them from wooded hillsides along tributaries of the Republican River in northwestern Kansas and chalk bluffs along the Smoky Hill River and its tributaries in western Kansas. Cockrum (1952:188) also states that the western subspecies usually is found along rock ledges. I have seen houses of *campestris* along extensive outcrops of rock in western Kansas and also in juniper trees growing near the outcrops. Information regarding habitat preferences north of Kansas is scanty. Jones (1954:485) records *campestris* as living in dense thickets and uninhabited buildings in southwestern Nebraska. Bailey (1905:109) reported the subspecies, *baileyi*, living in caves and cliffs of the timbered canyons of north-central Nebraska.

The eastern woodrat has never been reported from southeastern Nebraska, although there are specimens in the University of Kansas Museum of Natural History collected one mile west of Vermillion, Marshall County, Kansas, only 19 miles south of the Nebraska border. To determine those environmental factors preventing further northward dispersal, I made several trips into northeastern Kansas and southeastern Nebraska (see Fig. 13).

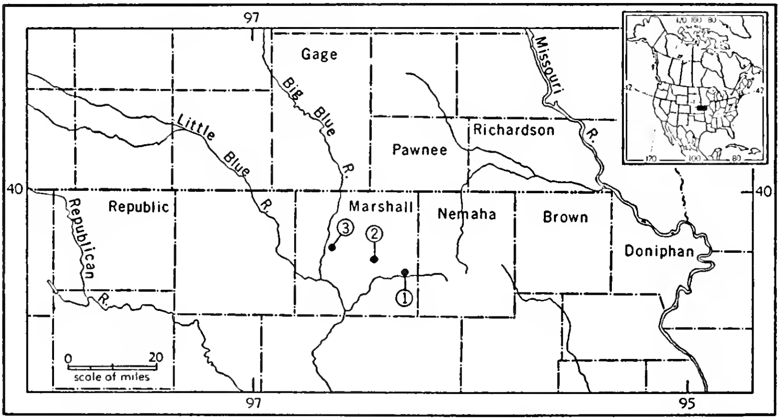


FIG. 13. Counties in northeastern Kansas and southeastern Nebraska investigated for occurrence of the eastern woodrat. Localities of known occurrence, all in Marshall County, are: (1) 1 mi. W Vermillion, (2) 5½ mi. S Beattie, (3) 2 mi. S Marysville.

In the summer of 1954, an intensive search was made for woodrats in Doniphan and Brown counties and in parts of Nemaha County. None was found. In eastern Marshall County, five and one-half miles south of Beattie, numerous houses were found in a large hedge row. The search was extended straight north from this locality into Nebraska. Several residents of Summerfield, Marshall County, Kansas, a small town at the Kansas-Nebraska border, could not recall having ever seen or heard of woodrats in the vicinity even though it was less than 15 miles from known stations of occurrence. Many miles of hedge rows were investigated in Pawnee and Richardson counties, Nebraska, but no sign of woodrats could be found. Testimony of several life-long residents all agreed that woodrats do not occur in those counties.

Geologic maps of Marshall County which show outcropping of Permian rock (Walters, 1954) indicate that a likely avenue into Nebraska would be along Big Blue River which courses through the western part of the county. Dr. Richard B. Loomis, who had done extensive field work in Gage County, Nebraska, reported outcropping rock to be fairly abundant along the terraces of Big Blue River for approximately six miles into Nebraska. These areas of rock, along small intermittent streams, as well as several hedge rows were searched thoroughly, but no sign of occupancy by woodrats past or present could be found. The ledges examined appeared suitable to support woodrats. However, it was noted that nearly all of the holes and crevices large enough to support woodrats were also large enough to offer shelter to opossums, skunks, and raccoons, and in almost every instance, had signs around them to indicate that they were in use by one of these larger mammals. Several long-abandoned houses, barns, and other buildings were investigated in this county, and in every instance, there was a total absence of sign. Shrubs and trees were noticeably sparse. In certain places, shale is exposed more than overlying limestone. Shale has never been observed to support woodrats.

The search was extended south into Kansas following the terraces. Rock ledges were seldom more than 100 yards long; gaps of up to two miles separated some of the exposures. Vegetation near the ground was sparse. Along a large rock ledge two miles south of Marysville, Marshall County, Kansas, woodrats were again found. Rock outcrops become much more nearly continuous south of this locality and are widespread over large areas. Vegetation on the slopes below the outcrops is usually dense owing to abundance of fragrant sumac and coralberry. Trees are principally burr oak and chestnut oak near the tops of the hills and elm near the bases. Even on hillsides which lack trees, fragrant sumac and dogwood form dense thickets near the crests of the hills. At the northern end of the Flint Hills, rimrock is abundant. The entire aspect of the habitat changes abruptly south of a line extending through the northern two-thirds of Marshall, Nemaha, Brown, and Doniphan counties. Topographically most of the area north of this line and on into Nebraska consists of till plains.

Hedge rows are not rare in northeastern Kansas and southeastern Nebraska, but they are, for the most part, short and isolated. In many instances they were found only on tops of low rolling hills. The land around them was open and lacked suitable cover for migrating. Trimming practices are widespread and result in thin rows lacking overhead protection. Only in the southern half of Marshall County were hedge rows found which were considered to be suitable for maintaining woodrats. This is probably correlated with agricultural practices. The southern part of the county is not cultivated for crops to the same extent as the northern part.

Seemingly, both physiographical and biological factors are limiting the spread of this woodrat through northeastern Kansas and into Nebraska. One of the major factors is the disruption of habitat, especially the outcropping rock, with intervening barriers of open country. In northeastern Kansas and southeastern Nebraska glacial till covers the bedrock with the result that an eroded rock-controlled topography is lacking except near the valley of the Kansas River to the south and Big Blue River to the west (Schoewe, 1949:289). The cuesta-type topography characteristic of eastern Kansas south of the Kansas River is mantled by this glacial drift. Areas remote from the major drainages are gently undulating, broad, and open. The bluffs along most of the streams are subdued. A similar situation also exists in the Nebraska counties. Outcrops along the Missouri River in Doniphan County are limited in occurrence and are not suitable for woodrats because they exist as a solid face of rock with no hiding places or shelter for houses. Outcrops along the Republican River that leaves Nebraska and enters north-central Kansas in Republic County could not be used as a migration route because of the nature of the rock. The exposures are shale, but most of northern Republic County is mantled by loess deposits which compose the surface material of the gently sloping plains. Rock that is more likely to support woodrats, the Dakota sandstone, crops out only in the southeastern corner of the county (Fishel, 1948:24).

In summary, scarcity of overhead cover limits the spread of populations of woodrats when discontinuous habitat is encountered. If it is assumed that intervening barriers are not absolute, flow across these barriers and subsequent establishment of populations would require a long period of favorable conditions because niches which are optimum are already filled by larger mammals. Immigrants would be forced into less than optimum habitat and it has been pointed out that considerable surpluses must exist before this occurs. It would take many years of favorable climate for woodrats to bridge gaps in sufficient numbers to establish populations in the suboptimum habitat of southeastern Nebraska. If this occurred in the past, a single period of climatic extreme may have destroyed the immigrants and the woodrats that had spread into the less favorable habitat near the origin of dispersal. A period of favorable years would then be required for numbers to increase enough again to fill less favorable habitats at marginal zones. Subsequently a still longer period would be required to recross the barriers. Just one rare climatic extreme of decimating effect could prevent populations from establishing themselves in Nebraska for a long period.

The Relation of Homeostasis to Survival

Among native North American small mammals, the eastern woodrat is notably euryecious. Extremes of temperature and of humidity are encountered within its range, with such hazards as recurrent floods, dust storms and blizzards. The species must cope also with an impressive array of enemies among which man is potentially the most dangerous.

Homeostasis, or the ability to exert controlling influences on the physical environment, has been expanded from its original meaning of maintaining physiological stability on the cellular level and established as an ecological principle (Allee, *et al.*, 1949:672). The plasticity of woodrats in general and of the eastern woodrat specifically to respond to the wide variety of conditions that occur throughout the range is directly correlated with this ability to modify the environment and make it relatively stable. The instinct to construct elaborate stick houses is an adaptive response making the animal less dependent on physical factors and certain biotic factors of the environment. Few mammals have progressed as far as woodrats have in this respect. Because of the protection afforded by the house, limits of tolerance to the environment have been broadened allowing invasion of new habitats. Some other mammals, for example the beaver and the muskrat, construct houses, but they do not live under the wide range of environmental conditions that woodrats do. Several harvest mice (*Reithrodontomys*) build shelters, but again they are more limited in habitats that they can occupy. The pika (*Ochotona*) is specialized in its manner of storing and "curing" hay, but in North America its range of habitat is limited to talus and similar situations.

The house of a woodrat not only offers protection against natural enemies, but creates a relatively stable microenvironment inside the house, which to a large degree offsets the fluctuations of the macroenvironment outside, and permits the woodrat to reproduce, rear its young, and feed successfully. In general, a stable environment is the key to success of animals.

Homeostasis existing among woodrats can be interpreted as "colonistic" under certain situations, but it is not the same type of adaptive response found in many social insects. As woodrats are not socialistic in behavior, colonistic homeostasis arises only secondarily. The colony of woodrats in the woodland part of the study area may be used as an illustration. Plant growth was initiated and sustained within the confines of the colony owing to presence of the woodrats, because seeds accidentally discarded by the rats from food stores sprouted and grew and because moisture retained in the mulch beneath the houses favorably affected plant growth. Increased density of vegetation gave added protection from climatic factors such as heat, wind, and rain. Although the magnitude of such protection is not great, it is advantageous in this way. The physiological functioning of the population would be toward relative stability.

Hooper (1949:25) suggests that *Neotoma* is characteristic of the arid mountains, interior plains, basins, and plateaus of the western United States and Mexico. There, limitations on natural cover would increase the need for developing means of protection. Hooper (1954:12) suggests also that the diminutive cricetine rodents of the monotypic genus, *Nelsonia,* which live among rocks in parts of Mexico, furnish a clue to the ancestry of woodrats. Hooper stated: "Morphologically, ecologically, and geographically it (*Nelsonia*) meets many of the requirements that might be expected in an ancestor of *Neotoma*." If the ancestral woodrats were smaller than present members of the genus, it may be postulated that the ability of woodrats to modify their environment results from the evolution of an exoadaptive (hereditary adjustment to the external environment) behaviorism, which paralleled morphological evolution. An increase in size may have increased vulnerability to enemies because there probably were fewer natural retreats of proper size. It may be further postulated that the drive to store food was developed in conjunction with building of houses. Without food stored in a house, reluctance to stray from shelter would necessitate quick trips and return to shelter to eat. A striking example of convergent evolution between woodrats in North America and stick-nest rats of the genus *Leporillus* in Australia may be attributed to similar requirements for shelter. Two species, *L. conditor* Sturt and *L. apicalis* Gould, inhabit the arid plains, and the third, *L. jonesi* Thomas, is an island dwelling species that sometimes lives in cliffs (Troughton, 1947:309-312). The members of the genus build large stick houses with elaborate systems of tunnels and one or two grass nests. These animals are nocturnal, vegetarian, and carry young suspended from the nipples of the mother. They store food, collect bones, and adorn the tops of their stick houses with rocks. They resemble woodrats in external appearance in having large ears and soft pelage.

Because of its inherent ability to build houses, the eastern woodrat is in a much better position to respond to nongenetic adaptations than it would be otherwise. Individual ontogenetic adaptations such as filling niches where houses are not required would be in this category. Utilization of a burrow made by another animal probably would be an acquired adaptation for a woodrat. The instinct of the species to build houses may be necessary in order that the rat have retreats of proper size within its area of activity; natural retreats of appropriate size are limited in occurrence. Even with the phylogenetic development of homeostatic ability, new habitats are not always open to invasion. There must be naturally occurring support for construction of houses if they are needed in lieu of other shelter. Woodrats do not disperse uniformly in all directions from a point of origin but follow natural avenues which possess the requirements for shelter and supports for houses. These avenues in eastern Kansas are linear in nature but have a dendritic pattern.

The Role of the Woodrat in Community Ecology

An assemblage consisting of woodrats and other natural populations of plants and animals in a specified area may be considered a major community.

Larger animals including predators such as snakes, owls, opossums, raccoons, skunks, foxes, and coyotes range over adjacent communities but have important effects also on this particular community, being attracted to prey species, and intimately participate in community functioning if adapted to utilize space among the rocks for shelter. In eastern Kansas fragrant sumac, dogwood, and coralberry might well be designated as characteristic of outcrops.

Woodrats influence plant growth, perhaps more than they do any of the other groups of organisms and alter the entire physiognomy of the vegetation. Feeding and storing activities of woodrats retard some plants and propagate others. Increased growth of plants in association with houses of woodrats increases ground humus which has a reciprocal effect on vegetation and biomass of the substratum. Moisture-retaining qualities of the matrix beneath woodrat houses have important effects not only on plant life but also on arthropod populations. Woodrats compete importantly with other vertebrates for space and food. Woodrat houses attract casual migrants such as birds, and foraging for them is better around woodrat houses than elsewhere. Woodrat houses often are preferred shelter of white-footed mice and skinks.

On a natural area as large as the Natural History Reservation woodrats are important in the "total" ecology for the reasons given above, and, in addition, in periods of peak abundance of woodrats, predators would perhaps be attracted to the area in exceptionally large numbers. If all niches occupied by woodrats were permanently vacated, white-footed mice would benefit because of more space and possibly more food. Some other kinds of animals would suffer because of their near obligatory symbiotic relations (house commensals) or loss of a source of food (predators).

SUMMARY

The eastern woodrat, *Neotoma floridana,* was studied in eastern Kansas over a period of four and one-half years. A program of live-trapping was conducted on a study area of approximately 58 acres in northeastern Douglas County, Kansas, in 1951, 1952, 1953, and part of 1954. In this period, 105 woodrats (47 females and 58 males) were live-trapped 660 times. Supplementary data were obtained from numerous areas elsewhere in eastern Kansas. The eastern woodrat is a highly plastic species, occupying habitats ranging from swamps to arid regions characterized by xerophytic vegetation. In eastern Kansas, habitat is of two major types, rock outcrops and planted osage orange hedge rows; hedge rows are the more important. Habitats of lesser importance are: rock fences, brush piles, thickets along streams, woodlands, and uninhabited buildings. Choice of habitat is governed by type of shelter for construction of houses, for purposes of foraging, and for escaping enemies.

Construction of stick houses is characteristic of this species although size and shape vary according to nature of support. Houses in hedge rows are usually conical, but those at rock outcrops are

irregular in shape according to size and shape of the crevices that they fill. Structure varies from house to house, but most, except for those at rock outcrops, have a basic pattern of a system of tunnels above and below ground, a chamber for storing food, a nest, and a fecal depository. The measure of success of a house is the length of continual occupancy. Houses in unfavorable locations seldom are occupied continuously.

Although 31 different kinds of plants were found to be utilized by woodrats as food, leaves and fruit of the osage orange tree were the most important. A sufficient amount of food to supply needs in winter is collected and stored by the woodrats in autumn. The drive to store food dominates all other activities.

Males are generally hostile toward each other. Males and females are less hostile toward each other in the season of breeding than at other times. Fighting results in numerous wounds, of which torn ears are most common. Stamping of the hind feet in response to danger, anger, or annoyance, is the most characteristic sound produced by these woodrats. They are extremely sanitary in habits and especially meticulous in care of pelage.

One species of tick, three species of fleas, 12 species of chiggers, and one dipteran fly were found parasitizing the eastern woodrat. Only chiggers occurred in large numbers. Known natural enemies include pilot black snakes, spotted skunks, and coyotes. Circumstantial evidence exists for several other snakes, raptorial birds, and mammals. The spotted skunk is probably one of the most important predators. Woodrats escape from enemies by climbing trees or seeking shelter in holes, burrows, or crevices. Success in escaping depends on stereotyped behavior in following predetermined routes. Numerous injuries such as loss of parts of the tail are probably inflicted by enemies. Spiders and other arthropods, box turtles, five-lined skinks, Great Plains skinks, white-footed mice, and cottontails, often live in woodrat houses.

In eastern Kansas, woodrats do not breed throughout the year. Breeding is limited chiefly to the period from February through August. Number of young in a litter varies from one to six, but two is probably the most common number. Young grow rapidly until approximately three months of age, but adult size is not attained until approximately eight months of age. Survival of young was exceptionally poor in the period of study and may have been correlated with weather conditions. Woodrats were observed to undergo three changes in pelage before attaining adult pelage.

Numbers of woodrats on the study area were low at the start of the study and steadily decreased thereafter. They were near peak abundance in 1948, but they abruptly declined in the winter of 1949. The decline coincided with a rare climatic extreme—an ice storm that left a coating of ice that did not melt for 21 days. Low reproductive rate, depletion of productive females, natural enemies, and scarcity of optimum habitat, are probable factors preventing re-establishment of numbers. Discontinuous habitat is limiting the spread of populations into new areas. Surpluses must be present to bridge partial barriers, and in this area, surpluses live in sub-optimum habitat and are subjected to climatic extremes. In general, success of woodrats has been increased by the phylogenetic development of a homeostatic ability. Stick houses serve to modify environmental factors toward greater stability and allow invasion of new habitats. The ecologic requirements for shelter, for reproducing, and for feeding, are met more successfully because of the house.

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□

INDEX TO VOLUME 8

Abies, 34
abieticola, Dryocopus pileatus, 332
Acer, 35
  Negundo, 570
Acadian Flycatcher, 334
acadicus, Aegolius acadicus, 331
Acanthis flammea, 349
Accipiter,
  atricapillus, 318
  cooperii, 264, 318, 597
  gentilis, 318
  striatus, 318
  velox, 318
achrusterus, Turdus migratorius, 339
Acris gryllus, 426, 473
Actitis macularia, 324
activity,
  collared lizard, 223
  prairie vole, 400
acuta, Anas, 315
Aechmophorus occidentalis, 310
aëdon, Troglodytes, 337
Aegolius acadicus, 330
aestiva, Dendroica petechia, 343
aestivalis, Aimophila, 351
aestivum, Triticum, 578
affinis, Aythya, 316
Agelaius,
  arctolegus, 347
  fortis, 347
  phoeniceus, 347
Agelena naevia, 266
Agelenopsis naevia, 602
agilis, Oporornis, 345
Agkistrodon contortrix, 463, 473, 596
aikeni,
  Junco, 352
  Otus asio, 330
Ailanthus, 35
Aimophila,
  aestivalis, 351
  cassinii, 351
  illinoensis, 351
  ruficeps, 351
  scottii, 351
Aix sponsa, 315
Ajaia ajaja, 313
ajaja, Ajaia, 313
alascanus, Haliaeetus leucocephalus, 319
alascensis, Calcarius lapponicus, 353
alba,
  Crocethia, 326
  Tyto, 330
albeola, Bucephala, 316
albicollis, Zonotrichia, 187, 192, 353
albifrons,
  Anser, 314
  Sterna, 328
albigula, Neotoma, 439, 609, 610, 613
albus, Casmerodius, 311
alcyon, Megaceryle alcyon, 331
Alder Flycatcher, 334
alexandrinus, Charadrius, 323
Alligator, 35
Alnus, 35
alpestris, Eremophila alpestris, 335
alpina, Erolia, 325
alticola, Melospiza lincolnii, 353
altissimum, Cirsium, 367
amandava, Estrilda, 163, 170, 171, 172, 173, 184, 187, 189, 194, 200
Amblyrhynchus cristatus, 253
Ambrosia,
  artemisiifolia, 367, 554, 578
  trifida, 367
Amelanchier, 35
American,
  Bittern, 312
  Coot, 322
  Egret, 311
  elm, 552
  Knot, 325
  Magpie, 336
  Merganser, 317
  Raven, 173, 336
  Redstart, 346
  toad, 423, 469
  Woodcock, 323
americana,
  Aythya, 315
  Bucephala clangula, 316
  Certhia familiaris, 337
  Fulica americana, 322
  Grus, 321
  Mareca, 315
  Mycteria, 312
  Oidemia nigra, 317
  Parula, 343
  Phytolacca, 367
  Prunus, 368, 568, 578
  Recurvirostra, 326
  Spiza, 161, 163, 183, 187, 189, 191, 193, 194, 200, 206, 349
americanum, Mesocelium, 138
americanus,
  Bufo, 423, 473, 515
  Coccyzus, 603
  Coccyzus americanus, 329
  Mergus merganser, 317
  Numenius americanus, 324

Ammodramus,
  bairdii, 350
  perpallidus, 350
  savannarum, 350
Ammospiza,
  caudacuta, 351
  nelsoni, 351
amoena, Passerina, 349
amoenus, Carphophis, 457, 473
Amorpha canescens, 367, 554
Amphispiza,
  bilineata, 352
  deserticola, 352
Anas,
  acuta, 315
  carolinensis, 315
  cyanoptera, 315
  discors, 315
  fulvigula, 314
  maculosa, 315
  platyrhynchos, 314
  rubripes, 314
  septentrionalis, 315
  strepera, 315
Anasa tristis, 602
anastera, Eustala, 602
anatum, Falco peregrinus, 320
Ancistrodon, contortrix, 35, 133, 136, 407
Andropogon,
  Gerardi, 367, 551
  virginicus, 367
Anhinga,
  anhinga, 311
  leucogaster, 311
annectens, Neotoma, 613
Anolis
  carolinensis, 19, 136, 253
  sagrei, 253
annuus, Helianthus, 367, 524, 544
Anser,
  albifrons, 314
  frontalis, 314
ant, 124, 484, 489, 493, 494, 495, 496
ant-eating frog, 277, 433, 469, 602
  behavior, 281
  breeding, 285
  color and pattern, 296
  development, 289
  field study of, 277
  food habits, 300
  growth, 289
  home range, 298
  movements, 297
  predation on, 302
  temperature relations, 282
anthracinus, Eumeces, 73
Anthus,
  spinoletta, 340
  rubescens, 340
  spragueii, 340
antigens, preparation of, 186
Aphelocoma,
  arizonae, 336
  coerulescens, 336
  woodhouseii, 336
  ultramarina, 336
Aphenogaster, 116
apicalis, Leporillus, 639
aquaticus, Scalopus, 133, 407
Aquila,
  canadensis, 319
  chrysaëtos, 319
arachnids, 260
arborea, Spizella, 163, 170, 187
  Spizella arborea, 352
Archilochus colubris, 331
arcticus, Pipilo erythrophthalmus, 350
arctolegus, Agelaius phoeniceus, 347
Ardea,
  herodias, 311
  treganzai, 311
  wardi, 311
arenacea, Spizella pusilla, 352
Arenaria,
  interpres, 323
  morinella, 323
areolata, Gastrophryne, 278
argentatus, Larus, 327
argutula, Sturnella magna, 346
argutus, Rubus, 368
Arilus cristatus, 261
Aristida oligantha, 367
Arizona Jay, 336
arizonae,
  Aphelocoma ultramarina, 336
  Neotoma cinerea, 613
  Spizella passerina, 352
arizonensis, Acomatacarus, 267
arkansana, Rosa, 554
armadillo, 133
armifera, Gastrocopta, 121, 124
aromatica, Rhus, 551, 568, 573
artemisiae, Molothrus ater, 348
artemisiifolia, Ambrosia, 367, 554, 578
Artocarpus, 34
arvense, Lithospermum, 367
arvensis, Convolvulus, 367
ash, prickly, 502
Ash-throated Flycatcher, 333
asio, Otus, 330
Asio,
  flammeus, 330
  otus, 330, 401
  wilsonianus, 330
aspersa, Lycosa, 262
Asyndesmus lewis, 332
ater,
  Molothrus, 163, 170, 184, 187, 189, 192, 193, 194, 200
  Molothrus ater, 348
athalassos, Sterna albifrons, 328
atratus, Coragyps, 318
atricapilloides, Parus carolinensis, 337

atricapillus,
  Accipiter gentilis, 318
  Parus, 603
  Parus atricapillus, 337
  Vireo, 341
atricilla, Larus, 327
attenuatus, Ophisaurus, 122, 444
attwateri, Neotoma floridana, 541
audax, Phidippus, 260, 602
Audubon Warbler, 343
auduboni, Dendroica auduboni, 343
aura, Cathartes, 317
auratus, Colaptes auratus, 332
auriceps, Crotaphytus collaris, 216, 223, 255
auricollis, Icteria virens, 346
auritus,
  Colymbus, 310
  Phalacrocorax auritus, 311
aurocapillus, Seiurus aurocapillus, 345
avens, 554
Avocet, 326
Aythya,
  affinis, 316
  americana, 315
  collaris, 316
  marila, 316
  nearctica, 316
  valisineria, 316

baileyi,
  Crotaphytus collaris, 216, 264
  Neotoma floridana, 541
bairdii,
  Ammodramus, 350
  Erolia, 325
Baird,
  Sandpiper, 325
  Sparrow, 350
Bald Eagle, 319
Baldpate, 315
Baldwini, Vernonia, 367, 554
Baltimore Oriole, 347
Bank Swallow, 335
barbouri, Eumeces, 11, 12
Barn,
  Owl, 330
  Swallow, 335
Barred Owl, 330
barrier, 18
Bartramia longicauda, 324
Bay-breasted Warbler, 344
beameri, Cuterebra, 588
beaver, 637
beetle, 260, 484, 487, 493, 494, 495, 496
behavior,
  ant-eating frog, 281
  woodrat, 583
bellii, Vireo bellii, 341
Bell Vireo, 341
Belted Kingfisher, 331
bendirei,
  Falco columbarius, 320
  Loxia curvirostra, 350
benti, Loxia curvirostra, 350
Benzoin, 34
Bering Straits, 33
bernicla, Branta, 314
Betula, 34, 35
bewickii, Thryomanes bewickii, 338
Bewick Wren, 338
bicolor,
  Dendrocygna, 314
  Iridoprocne, 335
  Parus, 337, 603
bilineata, Amphispiza, 352
Biome,
  deciduous forest, 31, 32
  oak-wild turkey, 29
  Taiga, 29
Biotic Districts, 32
bird, 484, 493, 494
bislineata, Eurycea, 471
bittersweet, 525, 554, 568, 578
bivittatus, Melanoplus, 262
Black
  and White Warbler; 342
  Duck, 314
  iguana, 230
  nightshade, 554, 578
  oak, 504
  Rail, 322
  Tern, 328
  Vulture, 318
blackberry, 502
Black-bellied Plover, 323
Black-billed Cuckoo, 329
blackbirds, 346-348
Blackburnian Warbler, 344
Black-capped Chickadee, 337
  Vireo, 341
Black-crowned Night Heron, 312
Black-headed Grosbeak, 349
Black-necked Stilt, 326
Black-poll Warbler, 344
Black-throated Blue Warbler, 343
  Gray Warbler, 344
  Green Warbler, 344
  Sparrow, 352
Blarina brevicauda, 133, 303, 402, 407, 515, 604
Blue
  Goose, 314
  Grosbeak, 163, 170, 348
  Jay, 336, 603
Blue-gray Gnatcatcher, 340
blue-racer, 39, 401, 453, 596
blue-stem grass, 551
Blue-winged
  Teal, 315
  Warbler, 342
bobcat, 133
Bobolink, 346

Bob-white, 321
bocourti, Bufo, 425
Bohemian Waxwing, 340
Bohmiella wilsoni, 588
Bombycilla,
  cedrorum, 340
  garrulus, 340
  pallidiceps, 340
Bonaparte Gull, 328
Bonasa, umbellus, 320
borealis,
  Buteo jamaicensis, 318
  Colaptes auratus, 332
  Kaloula, 277
  Lanius excubitor, 341
  Numenius, 324
  Nuttallornis, 335
boreas, Bufo, 424
boreus, Myiarchus crinitus, 333
Botaurus lentiginosus, 312
Bouteloua curtipendula, 367
box, turtle, 438, 602
box-elder, 570
brachidactyla, Geothlypis trichas, 345
brachyrhynchos,
  Corvus, 173, 479, 603
  Corvus brachyrhynchos, 336
bracteata, Tradescantia, 367
Brant, 314
Branta,
  bernicla, 314
  canadensis, 313
  hrota, 314
  hutchinsi, 313
  interior, 314
  leucopareia, 313
  minima, 313
  moffitti, 313
  nigricans, 314
  parvipes, 314
Braun, Lucy, 31, 32
breeding,
  ant-eating frog, 285
  collared lizard, 238
  five-lined skink, 48
  woodrat, 526, 605, 607
brevicauda, Blarina, 133, 303, 402, 407, 515, 604
Brewer
  Blackbird, 347
  Sparrow, 352
breweri, Spizella breweri, 352
brewsteri, Empidonax traillii, 334
Broad-winged Hawk, 133, 319, 402, 597
brome, 484, 486, 494, 495, 496
bromia, Cyanocitta cristata, 336
Bromus,
  inermis, 364, 367, 397, 524
  japonicus, 367, 524
Bronzed Grackle, 348
brooding, five-lined skink, 63
brooksi, Hesperiphona, 349
Brown
  Creeper, 337
  Pelican, 311
  skink, 446
  snake, 458, 515
  Thrasher, 338, 603
Bubalornithinae, 207
Bubo,
  occidentalis, 330
  virginianus, 330, 402, 596
buccinator, Olor, 313
Bucephala,
  albeola, 316
  americana, 316
  clangula, 316
  islandica, 316
buckwheat, 578
Buff-breasted Sandpiper, 326
Buffle-head, 316
Bufo,
  americanus, 423, 473, 515
  bocourti, 425
  boreas, 424
  marinus, 425
  woodhousei, 426
bullfrog, 435
bullockii, Icterus bullockii, 347
Bullock Oriole, 347
bull snake, 39, 462, 469, 596
buntings, 348-354
burr oak, 552, 573, 578
Burrowing Owl, 330
bursapastoris, Capsella, 367
bursarius, Geomys, 280
bush clover, 554
Buteo,
  borealis, 318
  calurus, 318
  harlani, 318
  jamaicensis, 264, 318, 597
  kriderii, 318
  lagopus, 319
  lineatus, 318
  platypterus, 263, 319, 597
  regalis, 319
  s. johannis, 319
  swainsoni, 264, 319
Butorides virescens, 312

cachinnans, Gallinula chloropus, 322
caerulea,
  Florida caerulea, 312
  Guiraca caerulea, 348
  Polioptila caerulea, 340
caerulescens,
  Chen, 314
  Dendroica caerulescens, 343
cafer, Colaptes, 332
Calamospiza melanocorys, 163, 170, 350

Calcarius, 168
  alascensis, 353
  lapponicus, 163, 170, 183, 353
  ornatus, 354
  pictus, 353
calendula, Regulus calendula, 340
Calidris,
  canutus, 325
  rufa, 325
California Gull, 327
californicus,
  Colymbus caspicus, 310
  Icterus cucullatus, 347
  Larus, 327
  Lepus, 403
  Microtus, 386
californianus, Geococcyx, 329
calligaster, Lampropeltis, 133, 136, 462, 515
Calliope Hummingbird, 331
Callipepla,
  pallida, 321
  squamata, 321
calurus, Buteo jamaicensis, 318
Campanotus
  castaneus, 121
  herculaneus, 121, 262
campestris, Neotoma floridana, 541
Canada
  Goose, 313
  Warbler, 346
canadense, Teucrium, 367
canadensis,
  Aquila chrysaëtos, 319
  Branta, 313
  Cercis, 552
  Geum, 554
  Grus canadensis, 321
  Sitta, 337
  Wilsonia, 346
canescens, Amorpha, 367, 554
Canis,
  latrans, 402, 407, 598
  familiaris, 407
Cannabis sativa, 554
canutus, Calidris, 325
Canvas-back, 316
Capella,
  delicata, 324
  gallinago, 324
Cape May Warbler, 343
capillare, Panicum, 524
Caprimulgus,
  carolinensis, 331
  vociferus, 331
Capsella bursapastoris, 367
Cardinal, 163, 170, 187, 189, 191, 192, 193, 194, 348, 603
cardinalis,
  Richmondena, 163, 170, 187, 189, 191, 192, 193, 194, 603
  Richmondena cardinalis, 348
Carduelidae, 207
Carduelinae, 161, 207
Carex gravida, 367
carinatus, Leiocephalus, 230, 253
Carolina
  Chickadee, 337
  Paroquet, 329
  Wren, 338
carolina, Porzana, 322
carolinense, Solanum, 367, 578
carolinensis,
  Anas, 315
  Anolis, 19, 136, 253
  Caprimulgus, 331
  Conuropsis, 329
  Dumetella, 338, 603
  Gastrophryne, 287
  Microhyla, 278
  Pandion haliaetus, 320
  Pelecanus occidentalis, 311
  Sitta carolinensis, 337
  Zenaidura macroura, 329
carolinus,
  Centurus, 332
  Euphagus carolinus, 347
Carphophis, amoenus, 120, 122, 457, 473
Carpinus, 34
Carpodacus, 167
  frontalis, 349
  mexicanus, 349
  purpureus, 163, 170, 171, 172, 187, 189, 192, 194, 200, 349
carrion-flower, 524
Carya, 34, 35
Casmerodius,
  albus, 311
  egretta, 311
caspia, Hydroprogne, 328
Caspian Tern, 328
caspicus, Colymbus, 310
cassinii,
  Aimophila, 351
  Vireo solitarius, 342
Cassin
  Kingbird, 333
  Sparrow, 351
castanea, Dendroica, 344
Castanea, 34, 35
castaneus, Campanotus, 121
Catbird, 338, 603
catenifer, Pituophis, 462
caterpillar, 124
catesbeiana, Rana, 302, 435
Cathartes,
  aura, 317
  teter, 317
Catoptrophorus,
  inornatus, 324
  semipalmatus, 324
caudacuta, Ammospiza, 351

caurinus, Melanerpes erythrocephalus, 332
Cedar Waxwing, 340
cedrorum, Bombycilla, 340
Celastrus, scandens, 34, 524, 554, 568, 578
celata, Vermivora celata, 343
Celtis, occidentalis, 553, 554, 578
Cemophora, 133
centipede, 260
Centurus,
  carolinus, 332
  zebra, 332
Cercis, canadensis, 552
Certhia,
  familiaris, 337
  americana, 337
cerulea, Dendroica, 344
Cerulean Warbler, 344
Ceuthophilus, 118
Chaetura pelagica, 331
chapmani, Chordeiles minor, 331
Charadrius,
  alexandrinus, 323
  circumcinctus, 323
  hiaticula, 323
  melodus, 323
  semipalmatus, 323
  tenuirostris, 323
  vociferus, 323
check-list of the birds of Kansas, 309
Chelydra serpentina, 437
Chen,
  caerulescens, 314
  hyperborea, 314
  rossii, 314
cherry, 484, 487, 492, 494
chestnut oak, 552, 573, 578
Chestnut-backed Bluebird, 339
Chestnut-collared Longspur, 354
Chestnut-sided Warbler, 344
chickadees, 337, 603
Chigger, 592
Chimney Swift, 331
Chipping Sparrow, 352
Chlidonias,
  niger, 328
  surinamensis, 328
chloropus, Gallinula, 322
Chlorura chlorura, 163, 170, 350
Chondestes grammacus, 163, 170, 351
Chordeiles,
  chapmani, 331
  howelli, 331
  minor, 331
  sennetti, 331
chorus frog, 430, 469
chrysaëtos, Aquila, 319
Chrysopa sp. 602
chrysoptera, Vermivora, 342
Chuck-will's-widow, 331
cicada, 578
cinerascens, Myiarchus cinerascens, 334
cinerea, Neotoma, 610, 613
cinereoargenteus, Urocyon, 599
cinereus,
  Plethodon, 471
  Seiurus aurocapillus, 345
cinnamomea, Tringa solitaria, 324
Cinnamomum, 34
Cinnamon Teal, 315
circaezans, Galium, 554
circumcinctus, Charadrius melodus, 323
ciris, Passerina, 349
Circus,
  cyaneus, 264, 320, 597
  hudsonius, 320
Cirsium
  altissimum, 367
  undulatum, 578
cismontanus, Junco hyemalis, 352
Cistothorus,
  platensis, 338
  stellaris, 338
citrea, Protonotaria, 342
citrina, Wilsonia, 346
clamitans, Rana, 436
Clangula hyemalis, 316
clangula, Bucephala, 316
Clark Nutcracker, 337
Clay-colored Sparrow, 352
Cliff Swallow, 335
Climatic factors, 419
clover, bush, 554
clypeata, Spatula, 315
Cnemidophorus, 259
  sexlineatus, 122, 259, 445
  tigris, 259
coccineum, Polygonum, 371
Coccyzus,
  americanus, 329, 603
  erythropthalmus, 329
coerulescens, Aphelocoma, 336
coffee-tree, 39, 524
Colaptes,
  auratus, 331
  borealis, 332
  cafer, 332
  collaris, 332
  luteus, 332
colchicus, Phasianus, 321
coleopteran, 115
Colinus,
  taylori, 321
  virginianus, 321
collared lizard, 39, 215, 440, 466
  activity, 223
  breeding, 238
  copulation, 231, 232
  ecological study of, 215
  eggs, 235
  food habits, 259

collared lizard—*Concluded*
  growth, 237
  habitat, 218
  molt, 246
  numbers, 247
  pattern, 241
  recovery from injury, 244
  regeneration of tail, 244
  reproduction, 229
  temperature, 224
  territoriality, 250
collaris,
  Aythya, 316
  Colaptes cafer, 332
  Crotaphytus, 122, 215, 440
color and pattern, ant-eating frog, 296
color, woodrat, 543
Coluber constrictor, 136, 264, 401, 458, 473, 596
colubris, Archilochus, 331
Columba livia, 328
columbarius, Falco columbarius, 320
columbiana, Nucifraga, 337
columbianus, Olor, 313
Columbigallina passerina, 329
Colymbus,
  auritus, 310
  californicus, 310
  caspicus, 310
  cornutus, 310
  grisegena, 310
  holböllii, 310
commensals, of woodrat, 515, 601
Common
  Loon, 310
  Scoter, 317
  Tern, 328
communication, woodrat, 585
Comocercoides dukae, 138
compass plant, 544, 578
competitors, of woodrat, 601
Comptonia, 34, 35
conditor, Leporillus, 639
confinis, Pooecetes gramineus, 351
Conorhinopsylla nidicola, 591
constrictor, Coluber, 136, 264, 401, 458, 473, 596
Contopus,
  richardsonii, 335
  virens, 335
contortrix
  Agkistrodon, 463, 473, 596
  Ancistrodon, 133, 136, 407
Conuropsis,
  carolinensis, 329
  ludovicianus, 329
Convolvulus arvensis, 367
cookei, Sitta carolinensis, 337
cooperii, Accipiter, 264, 318, 597
Cooper Hawk, 133, 318, 402, 597
Copperhead, 39, 453, 596
copulation,
  collared lizard, 231, 232
  five-lined skink, 48
Coragyps atratus, 318
coralberry, 552, 554, 578
corax, Corvus, 173, 336
cormorants, 311
corn, 484, 486, 492, 494, 496, 578
Cornus, 35
  drummondii, 368, 524, 552
cornutus, Colymbus auritus, 310
coronata, Dendroica coronata, 343
corvids, 336-337
Corvus,
  corax, 173, 336
  cryptoleucus, 336
  sinuatus, 336
Corvus brachyrhyncos, 173, 336, 479, 603
  economics, 483
  food habits, 479
  pellets, 479
  roosts, 483
Corylus, 34
cottontail, 604
courtship, five-lined skink, 48
Cowbird, 163, 170, 184, 187, 189, 192, 193, 194, 200, 348
cranes, 321
Crataegus mollis, 34, 578
crayfish, 484, 489, 493, 494, 495, 496
creeper, Virginia, 554
Crematogaster, 301
Crested Flycatcher, 187, 192, 333
cricket, 115
cricket frog, 426, 469
crinitus, Myiarchus, 187, 192, 333
cristata, Cyanocitta, 326, 603
cristatus,
  Amblyrhynchus, 253
  Arilus, 261
Crocethia alba, 326
crossbills, 350
Crotalus horridus, 401, 465, 511, 514, 515, 596
Crotaphytus
  auriceps, 216, 223, 255
  baileyi, 216, 264
  collaris, 215, 440
  dickersonae, 216
  reticulatus, 216
Crotaphytus collaris, 122, 215, 440
  activity, 223
  breeding, 238
  copulation, 231, 232
  ecological study of, 215
  eggs, 235
  food habits, 259
  growth, 237
  habitat, 218
  molt, 246

Crotaphytus collaris—*Concluded*
    numbers, 247
    pattern, 241
    recovery from injury, 244
    regeneration of tail, 244
    reproduction, 229
    temperature, 224
    territoriality, 250
Coturnicops noveboracensis, 322
Coyote, 402, 598
Crotophaga sulcirostris, 330
Crow, 173, 336, 479, 603
    economics, 483
    food habits, 479
    pellets, 479
    roosts, 483
cryptoleucus, Corvus, 336
Cryptophagus, 602
Cryptotis parva, 134, 515
cryptus, Thryomanes bewickii, 338
Ctenosaura pectinata, 230, 253
cuckoos, 329-330
cucullatus,
    Icterus, 347
    Lophodytes, 317
cuesta, 39
cunicularia, Speotyto, 330
cupido, Tympanuchus, 320
currucoides, Sialia, 340
curtipendula, Bouteloua, 367
curvirostra, Loxia, 163, 170, 171, 172, 350
Cuterebra beameri, 588
cyanea, Passerina, 163, 170, 187, 349
cyaneus, Circus, 264, 320, 597
cyanocephalus,
    Euphagus, 347
    Gymnorhinus, 337
Cyanocitta,
    bromia, 336
    cristata, 326, 603
    cyanotephra, 336
    stelleri, 336
cyanoptera, Anas, 315
cyanotephra, Cyanocitta cristata, 336

Deciduous Forest Biome, 31, 32
deglandi, Melanitta deglandi, 317
dekayi, Storeria, 453
De Kay's snake, 447, 453, 466, 469
delawarensis, Larus, 327
delicata, Capella gallinago, 324
deltoides, Populus, 368
Dermacentor variabilis, 594
Dendrocopos,
    medianus, 333
    pubescens, 333
    scalaris, 333
    symplectus, 333
    villosus, 333
Dendrocygna,
    bicolor, 314
    helva, 314
Dendroica,
    aestiva, 343
    auduboni, 343
    caerulescens, 343
    castanea, 344
    cerulea, 344
    coronata, 343
    discolor, 344
    dominica, 344
    fusca, 344
    hooveri, 343
    magnolia, 343
    nigrescens, 344
    palmarum, 345
    pennsylvanica, 344
    petechia, 343
    pinus, 344
    rubiginosa, 343
    sonorana, 343
    striata, 344
    tigrina, 343
    townsendi, 344
    virens, 344
Deroceras laeve, 123
deserticola, Amphispiza bilineata, 352
Desmodium glutinosum, 524
Desmognathus, 469
development,
    ant-eating frog, 289
    woodrat, 604, 616
Diadophis, 120, 122
    punctatus, 455, 473, 603
Dickcissel, 161, 163, 183, 187, 189, 191, 193, 194, 200, 206, 349
dickersonae, Crotaphytus, 216
Didelphis
    marsupialis, 402, 407
    virginiana, 597
differentialis, Melanoplus, 262
difficilis, Empidonax difficilis, 335
Dillenia, 34
dioica, Gymnocladus, 524
discolor, Dendroica discolor, 345
discors, Anas, 315
dissaëptus, Telmatodytes palustris, 338
diversa, Euschöngastia, 593
dogwood, 39, 554, 568, 578
Dolichonyx oryzivorus, 346
domesticus,
    Felis, 402
    Passer, 163, 170, 171, 172, 173, 184, 187, 189, 194
    Passer domesticus, 346
dominica,
    Dendroica, 344
    Pluvialis dominica, 323
Dormancy, 470

Double-crested Cormorant, 311
doves, 328-329
Downy Woodpecker, 333
dragon fly, 115
dropseed, 554
drummondii Cornus, 368, 524, 552
Dryocopus,
  abieticola, 332
  pileatus, 332
Duck Hawk, 320
ducks, 314-317
dukae, Comocercoides, 138
Dumetella carolinensis, 338, 603

eagles, 319
Eared Grebe, 310
Eastern
  Bluebird, 339
  Goldfinch, 163, 170, 171, 172, 187, 192, 194, 350
  Kingbird, 333
  Meadowlark, 346
  Phoebe, 334
  Wood Pewee, 335
  woodrat, Neotoma floridana: natural history and ecology, 535
ecological observations on the woodrat, Neotoma floridana, 501
ecological study of the collared lizard (Crotaphytus collaris), 215
ecology of,
  collared lizard, 215
  five-lined skink, 3
  woodrat, 501, 535
economics, of crow, 483
Ectopistes migratorius, 329
eggs,
  collared lizard, 235
  five-lined skink, 54
eggshell, 484, 489, 493, 494, 495
egretta, Casmerodius albus, 311
Eider, 316
Elanoïdes, forficatus, 318
Elaphe, 35
  guttata, 133, 136
  obsoleta, 133, 401, 461, 473, 511, 515, 596
electrina, Retinella, 121, 124
elegans, Eumeces, 11, 12
  Gastrophryne, 279
  Rallus elegans, 321
  Xysticus, 602
elm, American, 552
Emberizinae, 161, 207
Emberizoides, 160
Empidonax,
  brewsteri, 334
  difficilis, 334
  flaviventris, 334
  hellmayri, 335
  minimus, 334
  oberholseri, 334
Empidomax—*Concluded*
  traillii, 334
  virescens, 334
English Sparrow, 163, 170, 171, 172, 173, 184, 187, 189, 194, 346
enthymia, Eremophila alpestris, 335
enucleator, Pinicola, 163, 170, 171, 172, 349
Eocene, 34
Epitedia wenmanni, 591
Eremophila,
  alpestris, 335
  enthymia, 335
  hoyti, 335
  leucolaema, 335
  praticola, 335
Erolia,
  alpina, 325
  bairdii, 325
  fuscicollis, 325
  melanotus, 325
  minutilla, 325
  pacifica, 325
Ereunetes,
  pusillus, 325
  mauri, 326
ericrypta, Melospiza georgiana, 353
erythrocephalus, Melanerpes erythrocephalus, 332
erythrogaster, Hirundo rustica, 335
erythrophthalmus,
  Coccyzus, 329
  Pipilo, 163, 164, 170, 177, 178, 179, 180, 181, 182, 187
  Pipilo erythrophthalmus, 350
erythrorhynchos, Pelecanus, 311
erythrospermum, Taraxacum, 367
escape reactions, woodrat, 599
Eskimo Curlew, 324
Estrilda, amandava, 163, 167, 170, 171, 172, 173, 184, 187, 189, 194, 200
Estrildinae, 161, 207
Eumeces, 10
  anthracinus, 73
  barbouri, 11, 12
  elegans, 11, 12
  fasciatus, 1, 227, 447, 473-515, 602
  inexpectatus, 11, 12, 16, 28, 61, 130
  laticeps, 61, 64, 76, 115, 116, 130, 136, 143
  latiscutatus, 11, 12, 13, 19, 33
  lynxe, 58
  marginatus, 11, 12
  obsoletus, 22, 139, 259, 264, 451, 473, 515, 603
  oshimensis, 11, 12
  septentrionalis, 19, 77, 91, 452
  skiltonianus, 77, 91
  tamdaoensis, 11, 12
  tunganus, 11, 12, 33
  xanthi, 11, 12

Eumeces fasciatus, 3, 227, 447, 473-515, 602
  breeding, 48
  brooding, 63
  copulation, 48
  courtship, 48
  eggs, 54
  fighting, 51
  food habits, 115
  growth, 76
  habitat, 37
  hatchlings, 72
  home range, 100
  life history and ecology, 3
  movements, 99
  pattern changes, 91
  phenology, 44
  population, 139
  seasonal occurrence, 41
  sexual cycle, 44
  temperature relations, 18
  testes, 45
eumecis, Oöchoristica, 138
Euphagus,
  carolinus, 347
  cyanocephalus, 347
euphonia, Melospiza melodia, 353
Euphorbia marginata, 367, 554
Eupoda montana, 323
European Widgeon, 315
Eurycea, bislineata, 470, 471
Euschöngastia
  diversa, 593
  peromysci, 593
  setosa, 593
Eustala anastera, 602
Evening Grosbeak, 163, 170, 171, 172, 349
excubitor, Lanius, 341
excubitorides, Lanius ludovicianus, 341
exilis, Ixobrychus exilis, 312

Fagus, 34, 35
Falco,
  anatum, 320
  bendirei, 320
  columbarius, 320
  mexicanus, 264, 320
  obsoletus, 320
  peregrinus, 320
  richardsonii, 320
  rusticolus, 320
  sparverius, 264, 320
falcons, 320
Fall Line, 15
fallax, Neotoma mexicana, 613
false indigo, 220
familiaris,
  Canis, 407
  Certhia, 337
farneri, Pseudoschöngastia, 593
fasciatus, Eumeces, 1, 227, 447, 473-515, 602
faxoni, Hylocichla guttata, 339
fedoa, Limosa, 326
Felis domesticus, 402
femoral pores, 230
femur-rubrum, Melanoplus, 262
Ferruginous Rough-leg, 319
Field Sparrow, 352, 603
field study of ant-eating frog, 277
fighting, in five-lined skink, 51
finches, 348-354
fish, 484, 493, 494, 495
Fitch, Henry S.,
  A field study of the Kansas ant-eating frog, Gastrophryne olivacea, 277
  An ecological study of the collared lizard (Crotaphytus collaris), 215
  Life history and ecology of the five-lined skink, Eumeces fasciatus, 3
  Temperature responses in free-living amphibians and reptiles of northeastern Kansas, 419
five-lined skink, 446, 466, 469, 602
  breeding, 48
  brooding, 63
  copulation, 48
  courtship, 48
  eggs, 54
  fighting, 51
  food habits, 115
  growth, 76
  habitat, 37
  hatchlings, 72
  home range, 100
  life history and ecology, 3
  movements, 99
  pattern changes, 91
  phenology, 44
  population, 139
  seasonal occurrence, 41
  sexual cycle, 44
  temperature relations, 18
  testes, 45
flamingo, 313
flammea, Acanthis flammea, 349
flammeus, Asio flammeus, 330
flava, Triodia, 367, 397
flavifrons, Vireo, 341
flavipes, Totanus, 325
flaviventris, Empidonax, 334
fleas, 591
Florida
  caerulea, 312
  Gallinule, 322
floridana, Neotoma, 501, 535, 613
floridanus, Syvilagus, 407, 604
flycatchers, 333-335

food habits,
  ant-eating frog, 300
  collared lizard, 259
  crow, 479
  five-lined skink, 115
  prairie vole, 397
  woodrat, 524
foot, of skink, 7
forficata, Muscivora, 333
forficatus, Elanoïdes forficatus, 318
formosus, Oporornis, 345
forsteri, Sterna, 328
Forster Tern, 328
fortis, Agelaius phoeniceus, 347
fox, 133
  grape, 525
  gray, 599
  red, 402, 599
  Sparrow, 163, 170, 353
  squirrel, 604
fragrant sumac, 220, 551, 568
Franklin Gull, 327
Fregata,
  magnificens, 311
  rothschildi, 311
frenata, Mustela, 402, 596
Fringillidae, 159
Fringillinae, 161, 207
frog,
  ant-eating, 277, 433, 469, 602
  cricket, 426, 469
  chorus, 430, 469
  green, 436
frontalis,
  Anser albifrons, 314
  Carpodacus mexicanus, 349
Fulica americana, 322
fulicarius, Phalaropus, 326
fusca, Dendroica, 344
fuscescens, Hylocichla, 339
fuscicollis, Erolia, 325
fuscipes, Neotoma, 512, 539, 582, 609, 613
fulva, Vulpes, 402, 599
fulvigula, Anas, 314
Fulvous Tree-duck, 314

Gadwall, 315
gait, woodrat, 545
galbula, Icterus, 347
Galium, circaezans, 554
gallinago, Capella, 324
Gallinula,
  cachinnans, 322
  chloropus, 322
gallopavo, Meleagris, 321
Gambelia wislizenii, 227
gambelii, Zonotrichia leucophrys, 353
garden toad, 426
garrulus, Bombycilla, 340
garter snake, 453, 466
Gastrocopta armifera, 121, 124
Gastrophryne
  areolata, 278
  carolinensis, 287
  elegans, 279
  mazatlanensis, 279, 287
  olivacea, 278, 433, 473, 515, 602
  pictiventris, 279
  texensis, 278
  usta, 279
Gastrophryne olivacea,
  behavior, 281
  breeding, 285
  color and pattern, 296
  development, 289
  field study of, 277
  food habits, 300
  growth, 289
  home range, 298
  movements, 297
  predation on, 302
  temperature relations, 282
Gaultheria, 35
Gavia, immer, 310
  stellata, 310
geese, 313-314
gentilis, Accipiter, 318
Geococcyx californianus, 329
Geomys bursarius, 280
grouse locust, 124
georgiana, Melospiza georgiana, 353
georgica, Strix varia, 330
Geospizinae, 160, 207
Geothlypis,
  brachidactyla, 346
  occidentalis, 346
  trichas, 345
Gerardi, Andropogon, 367, 551
getulus, Lampropeltis, 133, 136, 462
Geum, canadensis, 554
gilvus, Vireo gilvus, 342
ginkgo, 34
glabra, Rhus, 554, 568
glass snake, 444
Glaucous Gull, 327
Gleditsia triacanthos, 368, 524, 551, 578
glutinosum, Desmodium, 524
Glyptostrobus, 34, 35
goatsuckers, 331
Golden
  Eagle, 319
  Plover, 323
Golden-crowned Kinglet, 340
Golden-eye, 316
goldenrod, 554, 578
Golden-winged Warbler, 342
gooseberry, 39
Goshawk, 318
gracilis, Micrathena, 602
gramineus, Pooecetes gramineus, 351
grammacus, Chondestes, 163, 170, 351
  Chondestes grammacus, 351

grammarus, Otospermophilus, 390
grape, 39, 492, 494, 495, 578
  fox, 525
grass, blue-stem, 551
grasshopper, 124, 260, 484, 488, 493, 494, 495, 496
Grasshopper Sparrow, 350
grass, tickle, 524
gravida, Carex, 367
gray squirrel, 604
Gray-cheeked Thrush, 339
Great
  Blue Heron, 311
  Lakes, 31
  Plains, skink, 466, 469, 603
Greater
  Prairie Chicken, 320
  Scaup Duck, 316
  Yellow-legs, 325
grebes, 310
Green Heron, 312
green frog, 436
greenbriar, 39, 554, 578
Green-tailed Towhee, 163, 170, 350
Green-winged Teal, 315
grisegena, Colymbus, 310
griseus,
  Limnodromus, 325
  Vireo, 341
Groove-billed Ani, 330
grosbeaks, 348-349
Ground Dove, 329
grouse, 320-321
growth,
  ant-eating frog, 289
  collared lizard, 237
  five-lined skink, 76
  prairie vole, 388
  woodrat, 527, 616
Grus,
  americana, 321
  canadensis, 321
  tabida, 321
Guiraca,
  caerulea, 163, 170, 348
  interfusa, 348
gulls, 327-328
gulosa, Lycosa, 602
guttata,
  Elaphe, 133, 136
  Hylocichla, 339
  Poephila, 163, 170, 173, 184, 187, 189, 194, 200
Gryllus pennsylvanicus, 116
gryllus, Acris, 426, 473
Gymnocladus dioica, 524
Gymnorhinus cyanocephalus, 337
Gyrfalcon, 320
habitat,
  collared lizard, 218
  five-lined skink, 37
  prairie vole, 366
  woodrat, 502, 545
hackberry, 553, 554, 578
haemastica, Limosa, 326
haematoreia, Neotoma floridana, 541
Hairy Woodpecker, 333
Haldea valeriae, 458
Haliaeetus,
  alascanus, 319
  leucocephalus, 319
haliaetus, Pandion, 320
Hamamelis, 34
harlani, Buteo jamaicensis, 318
Harris
  Hawk, 319
  Sparrow, 163, 170, 187, 189, 192, 194, 603
harrisi, Parabuteo unicinctus, 319
harvestman, 124
hasbroucki, Otus asio, 330
hatchlings, five-lined skink, 72
Hausmannia, 34
haw, red, 578
Hawaiia minuscula, 121
Hawk Owl, 330
hawks, 318-320
haydeni, Microtus ochrogaster, 378
hedonic function of femoral pores, 230
Helianthus, annuus, 367, 524
hellmayri, Empidonax difficilis, 335
helluo, Lycosa, 602
Helmintheros vermivorus, 342
helva, Dendrocygna bicolor, 314
Hemlock-white Pine-Northern Hardwoods Association, 30
hendersoni, Limnodromus griseus, 325
henslowii, Passerherbulus henslowii, 351
Henslow Sparrow, 351
herbacea, Smilax, 524
herculaneus, Campanotus, 121, 262
Hermit Thrush, 339
herodias, Ardea herodias, 311
herons, 311-312
Herpyllus vasifer, 602
Herring Gull, 327
Hesperiphona, 167
  brooksi, 349
  vespertina, 163, 170, 171, 172, 349
hiaticula, Charadrius, 323
hibernation, 18
hickory, 39
hiemalis, Troglodytes troglodytes, 337
Himantopus mexicanus, 326
himantopus, Micropalama, 325

Hirundo,
  erythrogaster, 335
  rustica, 335
hirundo, Sterna hirundo, 328
hispidus, Sigmodon, 368
hoactli, Nycticorax nycticorax, 312
holböllii, Colymbus grisegena, 310
homeostasis, woodrat, 637
home range,
  ant-eating frog, 298
  five-lined skink, 100
  prairie vole, 380, 382
  woodrat, 517
honey locust, 39, 502, 524
honey-shuck, 551, 573, 578
Hooded
  Merganser, 317
  Oriole, 347
  Warbler, 346
hooveri, Dendroica coronata, 343
Horned
  Grebe, 310
  Lark, 335
  Owl, 330, 402, 596
horridus, Crotalus, 401, 465, 511, 514, 515, 596
horse nettle, 525, 578
House
  Finch, 349
  Wren, 337, 603
houses, of woodrat, 560
howelli, Chordeiles minor, 331
hoyti, Eremophila alpestris, 335
hrota, Branta bernicla, 314
Hudsonian,
  Curlew, 324
  Godwit, 326
hudsonia, Pica, pica, 336
hudsonius,
  Circus cyaneus, 320
  Zapus, 407, 604
hummingbirds, 331
hungerfordi, Pseudoschöngastia, 593
hutchinsi, Branta canadensis, 313
Hydranassa,
  ruficollis, 312
  tricolor, 312
Hydroprogne caspia, 328
hyemalis,
  Clangula, 316
  Junco, 163, 170, 187, 189, 194, 200, 603
  Junco hyemalis, 352
hyperborea, Chen hyperborea, 314
hyperboreus, Larus, 327
hypugea, Speotyto cunicularia, 330
Hyla versicolor, 428, 473
Hylocichla,
  faxoni, 339
  fuscescens, 339
  guttata, 339
  minima, 339
  mustelina, 339
  salicicola, 339
  sequoiensis, 339
  swainsoni, 339
  ustulata, 339

ibises, 312-313
Icteria,
  auricollis, 346
  virens, 346
Icteridae, 161
Icterus, 184
  bullockii, 347
  californicus, 347
  cucullatus, 347
  galbula, 347
  spurius, 347
Ictinia misisippiensis, 318
iguana, black, 230
Iguanidae, 229
iliaca, Passerella iliaca, 353
illinoensis, Aimophila aestivalis, 351
  Neotoma floridana, 541
immer, Gavia, 310
Inca Dove, 329
inca, Scardafella, 329
Indigo Bunting, 163, 170, 187, 349
indigo, false, 220
inermis, Bromus, 364, 367, 397, 524
inexpectatus, Eumeces, 11, 12, 16, 28, 61, 130
inornatus, Catoptrophorus semipalmatus, 324
insects, 487
insolation, 419
interfusa, Guiraca caerulea, 348
interior, Branta canadensis, 314
interpres, Arenaria, 323
interrupta, Spilogale, 136
invictus, Lanius excubitor, 341
Iridoprocne bicolor, 335
ironweed, 554
islandica, Bucephala, 316
Ivy, poison, 554
Ixobrychus exilis, 312
Ixodes ricinus, 139
Ixoreus,
  naevius, 339
  meruloides, 339

jaegers, 327
jamaicensis,
  Buteo, 264, 318, 597
  Laterallus jamaicensis, 322
  Oxyura, 317

jamesi, Pedioecetes phasianellus, 321
japonica, Lonicera, 366
japonicus, Bromus, 367, 524
jays, 336-337
jonesi, Leporillus, 639
Jordan's Rule, 13
juddi, Melospiza melodia, 353
jumping mouse, 604
Junco,
  aikeni, 352
  cismontanus, 352
  hyemalis, 163, 170, 187, 189, 194, 200, 352, 603
  mearnsi, 352
  montanus, 352
  oreganus, 352
juncos, 352, 603

Kaloula borealis, 277
Kentucky Warbler, 345
Keteleria, 35
Killdeer, 323
King
  Eider, 316
  Rail, 321
king snake, 39, 462
kingfisher, 331
kinglets, 340
kites, 318
Kittiwake, 328
Kolreaueria, 34, 35
kriderii, Buteo jamaicensis, 318

labyrinthica, Strobilops, 121
laciniatum,
  Silphium, 554
Ladder-backed Woodpecker, 333
laeve, Deroceras, 123
lagopus, Buteo, 319
Lampropeltis,
  calligaster, 133, 136, 462, 515
  getulus, 133, 136, 462
  triangulum, 133, 136, 462, 515
Lanius,
  borealis, 341
  excubitor, 341
  excubitorides, 341
  invictus, 341
  ludovicianus, 341
  migrans, 341
lapidicina, Pardosa, 119
Lapland Longspur, 163, 170, 183, 353
lapponicus,
  Calcarius, 163, 170, 183
  Calcarius lapponicus, 353
lark, 335
Lark Bunting, 163, 170, 350
  Sparrow, 163, 170, 351
Larus,
  argentatus, 327
  atricilla, 327
  californicus, 327
Larus—*Concluded*
  delawarensis, 327
  hyperboreus, 327
  philadelphia, 328
  pipixcan, 327
  smithsonianus, 327
laterale, Lygosoma, 446
Laterallus jamaicensis, 322
laticeps, Eumeces, 61, 64, 76, 115, 116, 130, 136, 143
latiscutatus, Eumeces, 11, 12, 13, 19, 33
latrans, Canis, 402, 407, 598
Laughing Gull, 327
Lazuli Bunting, 349
leai, Stenotrema, 602
Least
  Bittern, 312
  Flycatcher, 334
  Sandpiper, 325
  Tern, 328
leadplant, 554
Leconte Sparrow, 351
leg-musculature, 177, 178, 179, 180, 181, 208
Leiobunum vittatum, 121, 602
Leiocephalus carinatus, 230, 252
lentiginosus, Botaurus, 312
lepida, Neotoma, 539, 613
Leporillus
  apicalis, 639
  conditor, 639
  jonesi, 639
Lepus californicus, 403
Lespedeza, 554
Lesser
  Prairie Chicken, 320
  Scaup Duck, 316
  Yellow-legs, 325
leucocephalus, Haliaeetus, leucocephalus, 319
leucogaster, Anhinga anhinga, 311
leucolaema, Eremophila alpestris, 335
leucopareia, Branta canadensis, 313
Leucophoyx thula, 311
leucophrys, Zonotrichia leucophrys, 353
leucoptera, Loxia leucoptera, 350
leucopterus, Mimus polyglottos, 338
leucopus, Peromyscus, 134, 372, 403, 407, 515, 541, 582, 603
Leucosticte, 167, 168
  tephrocotis, 163, 170, 171, 172, 183
Lewis Woodpecker, 332
lewis, Asyndesmus, 332
licorice, wild, 554
life history,
  and ecology of the five-lined skink, Eumeces fasciatus, 3
  prairie vole, 383
  woodrat, 535
light relations, woodrat, 559

limestone, Oread, 39, 221
limicola, Rallus limicola, 322
Limnodromus
  griseus, 325
  hendersoni, 325
  scolopaceus, 325
Limosa,
  fedoa, 326
  haemastica, 326
lineatus, Buteo lineatus, 319
lincolnii, Melospiza lincolnii, 353
Lincoln Sparrow, 353
lineatum, Tropidoclonion, 454, 473
lined snake, 454, 469
Liquidambar, 34, 35
Lithocarpus, 35
Lithospermum arvense, 367
litters,
  prairie vole, 386
  woodrat, 609
Little Blue Heron, 312
live-traps, 364, 540
livia, Columba, 328
lizard, collared, 39, 215, 440, 466
lobatus, Lobipes, 327
Lobipes lobatus, 327
locust, honey, 39, 502, 524
Loggerhead Shrike, 341
Long-billed
  Curlew, 324
  Dowitcher, 325
  Marsh Wren, 338
Long-eared Owl, 330, 401
longevity,
  prairie vole, 388
  woodrat, 530
longicauda,
  Bartramia, 324
  Toxostoma rufum, 338
longicaudus, Stercorarius, 327
longifolia, Physalis, 367
Longistriata, neotoma, 588
longspurs, 353-354
Long-tailed Jaeger, 327
Lonicera japonica, 366
loons, 310
Lophodytes cucullatus, 317
lotor, Procyon, 402, 598
Louisiana
  Heron, 312
  Water-thrush, 345
Loxia, 167
  bendirei, 350
  benti, 350
  curvirostra, 163, 170, 171, 172, 350
  leucoptera, 350
  minor, 350
  sitkensis, 350
  stricklandi, 350
luciana, Neotoma fuscipes, 613
ludoviciana, Piranga, 348
ludovicianus,
  Conuropsis carolinensis, 329
  Lanius, 341
  Pheucticus, 348, 603
  Thryothorus ludovicianus, 338
luteus, Colaptes auratus, 332
Lycosa,
  aspersa, 262
  gulosa, 602
  helluo, 602
  rabida, 262
Lygosoma laterale, 446
lynxe, Eumeces, 58

Macgillivray Warbler, 345
Maclura, pomifera, 39, 502, 524, 525, 549, 578
macrocarpa, Quercus, 552, 578
macrotis, Neotoma fuscipes, 613
macroura, Zenaidura, 329, 603
macularia, Actitis, 324
maculosa, Anas fulvigula, 315
magister, Neotoma, 539, 609, 613
magna, Sturnella magna, 346
magnificens, Fregata, 311
Magnolia, 34
Magnolia Warbler, 343
magnolia, Dendroica, 343
magpie, 336
Mahonia, 35
major, Plantago, 367
Mallard, 314
mammal, 484, 493, 494, 495, 496
mammalian associates, prairie vole, 403
Man-o'-war-bird, 311
Mareca,
  americana, 315
  penelope, 315
Marmota
  monax, 604
maniculatus, Peromyscus, 407
Marbled Godwit, 326
marginata, Euphorbia, 367, 554
marginatus, Eumeces, 11, 12
marginella, Zenaidura macroura, 329
marijuana, 554
marila, Aythya, 316
Marsh Hawk, 320, 597
marinus, Bufo, 425
marsupialis, Didelphis, 402, 407
Martin, Edwin P., A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas, 363
martinica, Porphyrula, 322
Masticophis taeniatus, 264
mauri, Ereunetes, 326
Mays, Zea, 578
mazatlanensis, Gastrophryne, 279, 287
McCown Longspur, 353
mccownii, Rhynchophanes, 353
meadowlarks, 346-347

mearnsi, Junco oreganus, 352
measurements, wood rat, 542
medianus, Dendrocopos pubescens, 333
Megaceryle, alcyon, 331
megalotis, Reithrodontomys, 134, 372, 404
Melanerpes,
  caurinus, 332
  erythrocephalus, 332
Melanitta,
  deglandi, 317
  perspicillata, 317
melanocephalus, Pheucticus melanocephalus, 348
melanocorys, Calamospiza, 163, 170, 350
melanoleucus, Totanus, 325
Melanoplus, 262
  bivittatus, 262
  differentialis, 262
  femur-rubrum, 262
melanotus, Erolia, 325
Meleagris,
  gallopavo, 321
  silvestris, 321
Melilotus, 222
melodia, Melospiza, 353, 603
melodus, Charadrius, 323
Melospiza,
  alticola, 353
  ericrypta, 353
  euphonia, 353
  georgiana, 353
  juddi, 353
  lincolnii, 353
  melodia, 353, 603
  montana, 353
Mentzelia, 222
Mephitis mephitis, 136, 402
mephitis, Mephitis, 136, 402
merganser, Mergus, 317
Mergus,
  americanus, 317
  merganser, 317
  serrator, 317
meruloides, Ixoreus naevius, 339
Mesocelium americanum, 138
Metasequoia, 35
Mexican Cormorant, 311
mexicana,
  Neotoma, 539, 613
  Plegadis, 313
  Sialia, 339
mexicanus,
  Carpodacus, 349
  Falco, 264, 320
  Himantopus, 326
  Phalacrocorax olivaceus, 311
Micrathena gracilis, 602
Microhyla
  carolinensis, 278
  olivacea, 116
micropus, Neotoma, 539, 598, 613
Micropalama himantopus, 325
Microtus
  californicus, 386
  haydeni, 378
  montanus, 390
  ochrogaster, 134, 281, 363
  pennsylvanicus, 363, 472
  pinetorum, 134, 363, 407
Microtus ochrogaster,
  activity, 400
  food habits, 397
  growth rates, 388
  habitat, 366
  home range, 380, 382
  life history, 383
  life span, 388
  litter size and weight, 386
  mammalian associates, 403
  population density, 476
  population structure, 373, 374
  predation on, 401
  reproduction, 383
  reproduction of, correlated with rainfall, 384, 385
  runways and nests, 398
  size, 388
Micrurus, 133
migrans, Lanius ludovicianus, 341
migratorius,
  Ectopistes, 329
  Turdus migratorius, 339
milo, 578
Mimus,
  polyglottos, 338
  leucopterus, 338
minima,
  Branta canadensis, 313
  Hylocichla minima, 339
minimus, Empidonax, 334
mink, 133
minor,
  Chordeiles minor, 331
  Loxia curvirostra, 350
  Philohela, 323
minuscula, Hawaiia, 121
minutilla, Erolia, 325
misisippiensis, Ictinia, 318
Mississippi Kite, 318
Mniotilta varia, 342
Mockingbird, 338
modestum, Phrynosoma, 259
moffitti, Branta canadensis, 313
moisture requirement, woodrat, 555
mole, 133
mollis, Crataegus, 578
mollissima, Somateria, 316

Molothrus, 160
  artemisiae, 348
  ater, 163, 170, 184, 187, 189, 192, 193, 194, 200, 348
molt, collared lizard, 246
monax, Marmota, 604
montana,
  Eupoda, 323
  Melospiza melodia, 353
montanus,
  Junco oreganus, 352
  Microtus, 390
  Oreoscoptes, 338
  Pipilo erythrophthalmus, 350
monticola, Oporornis tolmiei, 345
morinella, Arenaria interpres, 323
motacillus, Seiurus, 163, 170, 345
Mottled Duck, 314
Mountain
  Bluebird, 340
  Plover, 323
Mourning
  Dove, 329, 603
  Warbler, 345
mouse,
  jumping, 604
  white-footed, 583, 604
movements,
  ant-eating frog, 297
  five-lined skink, 99
  woodrat, 623
Muehlenbergii, Quercus, 552, 578
mullein, 554
muris, Trichuris, 588
Mus musculus, 407
Muscivora forficata, 333
Musculus,
  abductor digiti IV, 174
  adductor longus et brevis, 167
  biceps femoris, 166
  extensor digitorum longus, 168
  extensor hallucis longus, 174
  femorotibialis externus, 165
  femorotibialis internus, 165
  femorotibialis medius, 165
  flexor digitorum longus, 173
  flexor hallucis brevis, 174
  flexor hallucis longus, 173
  flexor perforans et perforatus digiti II, 172
  flexor perforans et perforatus digiti III, 172
  flexor perforatus digiti II, 171
  flexor perforatus digiti III, 171
  flexor perforatus digiti IV, 172
  gastrocnemius, 169
  iliacus, 164
  iliotibialis, 165
  iliotrochantericus anticus, 164
  iliotrochantericus medius, 164
  iliotrochantericus posticus, 164
  ischiofemoralis, 167
Musculus—*Concluded*
  lumbricalis, 175
  obturator internus, 167
  peroneus brevis, 169
  peroneus longus, 169
  piriformis, 165
  plantaris, 170
  sartorius, 164
  semimembranosus, 166
  tibialis anticus, 168
musculus, Mus, 407
muskrat, 637
Mustela frenata, 402, 596
mustelina, Hylocichla, 339
Myadestes townsendi, 340
Mycteria americana, 312
Myiarchus,
  boreus, 333
  cinerascens, 333
  crinitus, 187, 192, 333
Myology, 159
myology and serology of the Avian Family Fringillidae, a taxonomic study, 160
Myrica, 34
Myrtle Warbler, 343

naevia, Agelena, 266
naevia, Agelenopsis, 602
naevius,
  Ixoreus, 339
  Otus asio, 330
Nashville Warbler, 343
Natrix, 35
  sipedon, 302, 452
natural enemies, woodrat, 511
nearctica, Aythya marila, 316
neglecta, Sturnella neglecta, 347
Negundo, Acer, 570
Nelsonia, 638
nelsoni,
  Ammospiza, caudacuta, 351
  Sitta carolinensis, 337
Nelumbo, 34
Nemobius, 117
Neotoma,
  albigula, 539, 609, 610, 613
  annectens, 613
  arizonae, 613
  attwateri, 541
  baileyi, 541
  campestris, 541
  cinerea, 610, 613
  fallax, 613
  floridana, 501, 535, 613
  fuscipes, 512, 539, 582, 609, 613
  haematoreia, 541
  illinoiensis, 541
  lepida, 539, 613
  luciana, 613
  macrotis, 613
  magister, 539, 609, 613

Neotoma—*Concluded*
  mexicana, 539, 613
  micropus, 539, 598, 613
  osagensis, 541, 613
  rubida, 541, 613
  smalli, 541
  streatori, 613
  venusta, 613
  warreni, 613
neotoma, Longistriata, 588
Neotoma floridana, 501, 535, 613
  behavior, 583
  breeding, 526, 605, 607
  color, 543
  commensals, 515, 601
  communication, 585
  competitors, 601
  development, 604, 616
  ecology, 501, 535
  escape reactions, 599
  food habits, 524
  gait, 545
  growth, 527, 616
  habitat, 502, 545
  heat relations, 555
  homeostasis, 637
  home range, 517
  houses, 560
  life history, 535
  light relations, 559
  litter size and number, 609
  longevity, 530
  measurements, 542
  moisture requirements, 555
  movements, 623
  natural enemies, 511
  parasites, 588
  parturition, 614
  pelage, 587, 621
  population, 623, 631
  posture, 544
  predation on, 511
  reduction of population, 505
  reproduction, 604
  sanitation, 587
  senses, 586
  territoriality, 521
  weight, 543
  young, 615, 620
nettle, horse, 525, 578
nevadensis, Passerculus sandwichensis, 350
niceae, Thryomanes bewickii, 338
nidicola, Conorhinopsylla, 591
niger,
  Chlidonias, 328
  Sciurus, 603
Nighthawk, 331
nightshade, black, 554, 578
nigrescens, Dendroica, 344
nigricans, Branta, 314
nigrita, Pseudacris, 430, 454, 473
nigrum, Solanum, 554, 578
nivalis, Plectrophenax nivalis, 354
Northern Phalarope, 327
  Shrike, 341
  Water-thrush, 345
norvegicus, Rattus, 512
notabilis, Seiurus noveboracensis, 345
noveboracensis,
  Coturnicops noveboracensis, 322
  Seiurus, 345
  Vireo griseus, 341
nuchalis, Sphyrapicus varius, 332
Nucifraga columbiana, 337
numbers, collared lizard, 247
nuthatches, 337
nuttallii, Phalaenoptilus nuttallii, 331
Nuttallornis borealis, 335
Nyctanassa violacea, 312
Nyctea scandiaca, 330
Nycticorax
  nycticorax, 312
  hoactli, 312
Nyssa, 34, 35

oak,
  black, 504
  burr, 552, 573, 578
  chestnut, 552, 573, 578
Oak-hickory association, 32
Oak-wild turkey biome, 29
oats, 484, 485, 492, 494, 495, 496
oberholseri, Empidonax, 334
oblitus, Passerculus sandwichensis, 350
obsoleta, Elaphe, 133, 401, 461, 473, 511, 515, 596
obsoletus,
  Eumeces, 22, 139, 259, 264, 451, 473, 515, 603
  Falco rusticolus, 320
  Salpinctes obsoletus, 338
occidentalis,
  Aechmophorus, 310
  Bubo virginianus, 330
  Celtis, 553, 554, 578
  Geothlypis trichas, 346
  Pelecanus, 311
  Sceloporus, 253
Ochotona, 637
ochracea, Spizella arborea, 352
ochrogaster, Microtus, 134, 281, 363
Oidemia,
  americana, 317
  v. nigra, 317
Old-squaw, 316
oligantha, Aristida, 367
Oligocene, 34

olivacea,
    Gastrophryne, 278, 433, 473, 515, 602
    Microhyla, 116
    Piranga, 348
olivaceus,
    Phalacrocorax, 311
    Sceloporus, 253
    Vireo, 163, 168, 170, 174, 184, 342
Olive-backed Thrush, 339
Olive-sided Flycatcher, 335
Olor,
    buccinator, 313
    columbianus, 313
Onoclea, 34
Oöchoristica eumecis, 138
Opheodrys, 35
Ophisaurus attenuatus, 122, 444
Oporornis,
    agilis, 345
    formosus, 345
    monticola, 345
    philadelphia, 345
    tolmiei, 345
opossum, 133, 402, 597
Opuntia, 220
orange, Osage, 39, 502, 524, 525, 549, 578
Orange-crowned Warbler, 343
orbiculatus, Symphoricarpos, 368, 552 554, 578
Orchard Oriole, 347
Orchopeas sexdentatus, 591
Oread limestone, 39, 221
Oregon Junco, 352
oreganus, Junco, 352
Oreoscoptes montanus, 338
orestera, Vermivora celata, 343
orioles, 347
ornata, Terrapene, 438, 602
ornatus, Calcarius, 354
oryzivorus, Dolichonyx, 346
osagensis, Neotoma, 541, 613
Osage orange, 39, 502, 524, 525, 549, 578
oshimensis, Eumeces, 11, 12
Osprey, 320
osteoderm, of skink, 9
Oswaldocruzia pipiens, 138
Otospermophilus, grammarus, 390
Otus,
    aikeni, 330
    asio, 330
    hasbroucki, 330
    naevius, 330
    swenki, 330
otus, Asio, 330, 401
Oven-bird, 163, 170, 345
owl,
    long-eared, 401
    horned, 402, 596
owls, 330-331
Oxalis violacea, 367
Oxyura,
    jamaicensis, 317
    rubida, 317

pacifica, Erolia alpina, 325
Painted Bunting, 349
pallida,
    Callipepla squamata, 321
    Spizella, 352
pallidiceps, Bombycilla garrulus, 340
pallidicinctus, Tympanuchus, 320
pallidor, Passerina ciris, 349
Palm Warbler, 345
palmarum, Dendroica palmarum, 345
palustris, Telmatodytes, 338
Pandion,
    carolinensis, 320
    haliaetus, 320
Panicum
    capillare, 524
    virgatum, 367
Parabuteo,
    harrisi, 319
    unicinctus, 319
parasites, woodrat, 588
parasiticus, Stercorarius, 327
Parcoblatta, 116
Pardosa lapidicina, 119
parkmanii, Troglodytes aëdon, 337
Parula
    americana, 343
    Warbler, 343
Parthenocissus quinquefolia, 554
parturition, woodrat, 614
Parulidae, 207
Parulinae, 207
Parus,
    atricapilloides, 337
    atricapillus, 337, 603
    bicolor, 337, 603
    carolinensis, 337
    septentrionalis, 337
parva, Cryptotis, 134, 515
parvipes, Branta canadensis, 314
parvus, Numenius americanus, 324
Pasimachus, 261
Passenger Pigeon, 329
Passer, 167
    domesticus, 163, 170, 171, 172, 173, 184, 187, 189, 194, 346
Passerculus,
    nevadensis, 350
    oblitus, 350
    sandwichensis, 350
    savanna, 350
Passerella iliaca, 163, 170, 353
Passerherbulus,
    caudacutus, 351
    henslowii, 351

Passerina,
  amoena, 349
  ciris, 349
  cyanea, 163, 170, 187, 349
  pallidior, 349
passerina,
  Columbigallina, 329
  Spizella passerina, 352
Passerinae, 207
pattern,
  changes, five-lined skink, 91
  collared lizard, 241
pectinata, Ctenosaura, 230, 253
Pectoral Sandpiper, 325
Pedioecetes,
  jamesi, 321
  phasianellus, 321
pelage, of woodrat, 587, 621
pelagica, Chaetura, 331
Pelecanus
  carolinensis, 311
  erythrorhnychos, 311
  occidentalis, 311
pelicans, 311
pellets, of crow, 479
penelope, Mareca, 315
pennsylvanica, Dendroica, 344
pennsylvanicus,
  Gryllus, 116
  Microtus, 363, 472
peregrina, Vermivora, 342
peregrinus, Falco, 320
peromysci Euschöngastia, 593
Peromyscus,
  leucopus, 134, 403, 407, 541, 582, 603
  maniculatus, 407
perpallidus, Ammodramus savannarum, 350
Persea, 34
perspicillata, Melanitta, 317
petechia, Dendroica, 343
Petrochelidon pyrrhonota, 335
phaeopus, Numenius, 324
Phalacrocorax,
  auritus, 311
  mexicanus, 311
  olivaceus, 311
Phalaenoptilus nuttallii, 331
phalaropes, 326-327
Phalaropus fulicarius, 326
phasianellus, Pedioecetes, 321
Phasianus colchicus, 321
phenology, five-lined skink, 44
Pheucticus,
  ludovicianus, 348, 603
  melanocephalus, 348
Philohela minor, 323
Phidippus, 121, 260
  audax, 260, 602
Philadelphia Vireo, 342
philadelphia,
  Larus, 328
  Oporornis, 345
philadelphicus, Vireo, 342
Philetairus, 160
phoebe, Sayornis, 334
phoeniceus, Agelaius phoeniceus, 347
Phoenicopterus ruber, 313
Phrynosoma modestum, 259
Physalis longifolia, 367
Phytolacca americana, 367, 524
Pica,
  hudsonia, 336
  pica, 336
pica, Pica, 336
Picea, 34, 35
pictiventris, Gastrophryne, 279
pictus, Calcarius, 353
Pied-billed Grebe, 310
Pigeon Hawk, 320
pigeons, 328-329
pika, 637
Pileated Woodpecker, 332
pileatus, Dryocopus pileatus, 332
pileolata, Wilsonia pusilla, 346
pilot black snake, 39, 401, 461, 511, 513, 515, 596
Pine
  Grosbeak, 163, 170, 171, 172, 349
  Siskin, 349
  Warbler, 344
pinetorum, Microtus, 134, 363, 407
Pine-woods Sparrow, 351
Pinicola, 167
  enucleator, 163, 170, 171, 172, 349
pinnatus, Tympanuchus cupido, 320
Piñon Jay, 337
Pinus, 34, 35
pinus,
  Dendroica, 344
  Spinus pinus, 350
  Vermivora, 342
Pintail, 315
pipiens,
  Oswaldocruzia, 138
  Rana, 302, 436, 473
Pipilo,
  arcticus, 350
  erythrophthalmus, 163, 164, 170, 177, 178, 179, 180, 181, 182, 187, 350
  montanus, 350
Piping Plover, 323
pipits, 340
pipixcan, Larus, 327
Piranga, 184
  ludoviciana, 348
  olivacea, 348
  rubra, 163, 170, 183, 184, 187, 189, 200, 348
Pituophis catenifer, 462
Plantago major, 367

Plantanus, 34
platensis, Cistothorus, 338
Platt, Dwight, Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas, 479
platypterus, Buteo, 263, 597
    Buteo platypterus, 319
platyrhynchos, Anas platyrhynchos, 314
Plectrophenax nivalis, 354
Plegadis mexicana, 313
Pleistocene, 18, 30, 34
Plethodon, 470
    cinereus, 471
Ploceidae, 160, 207
Ploceinae, 207
plovers, 323
plum, wild, 568, 578
plumbeus, Vireo solitarius, 342
Pluvialis dominica, 323
Poa pratensis, 397
pocket gopher, 281
podiceps, Podilymbus, 310
    Podilymbus podiceps, 310
Poephila guttata, 163, 167, 170, 173, 184, 187, 189, 194, 200
pokeberry, 487, 495, 496, 525
poison Ivy, 554
Polioptila caerulea, 340
Polistes, 120
polyglottos, Mimus polyglottos, 338
Polygonum, 285
    coccineum, 371
    scandens, 578
Pomarine Jaeger, 327
pomarinus, Stercorarius, 327
pomifera, Maclura, 39, 502, 524, 525, 549, 578
Pooecetes,
    confinis, 351
    gramineus, 351
Poor-will, 331
population,
    density, prairie vole, 476
    five-lined skink, 139
    structure, prairie vole, 373, 374
    study of the prairie vole (Microtus ochrogaster) in northeastern Kansas, 363
    woodrat, 623, 631
Populus, 35
    deltoides, 368
Porphyrula martinica, 322
Porzana carolina, 322
posture, woodrat, 544
Prairie
    Falcon, 264, 320
    rat snake, 469
    skink, 469
    spotted skunk, 511, 512
    Warbler, 344
prairie vole, 281, 363
    activity, 400
    food habits, 397
    growth rates, 388
    habitat, 366
    home range, 380, 382
    life history, 383
    life span, 388
    litter size and weights, 386
    mammalian associates, 403
    population density, 476
    population structure, 373, 374
    predation on, 401
    reproduction, 383
    reproduction, correlated with rainfall, 384, 385
    runways and nests, 398
    size, 388
pratensis, Poa, 397
praticola, Eremophila alpestris, 335
pratincola, Tyto alba, 330
predation on,
    ant-eating frog, 302
    prairie vole, 401
    woodrat, 511
preparation of antigens, 186
prickly ash, 502
prinoides, Quercus, 524
Procyon lotor, 402, 598
Progne subis, 336
propinquus, Turdus migratorius, 339
Prothonotary Warbler, 342
Protonotaria citrea, 342
Prunus americana, 368, 568, 578
Pseudacris nigrita, 430, 454, 473
Pseudolarix, 35
Pseudoschöngastia
    farneri, 593
    hungerfordi, 593
Pseudotsuga, 35
Psittorostra, 160
Pterocarya, 35
Ptinus, 602
pubescens, Dendrocopos pubescens, 333
punctatus, Diadophis, 455, 473, 603
Purple
    Finch, 163, 170, 171, 172, 187, 189, 192, 194, 200
    Gallinule, 322
    Martin, 336
purpureus, Carpodacus, 163, 170, 171, 172, 187, 189, 192, 194, 200, 349
    Carpodacus purpureus, 349
pusilla,
    Spizella, 603
    Spizella pusilla, 352
    Wilsonia pusilla, 346
pusillus, Ereunetes, 325
putorius, Spilogale, 402, 511, 512, 591, 596

pyrrhonota, Petrochelidon pyrrhonota, 335
Pyrrhuloxinae, 207

quail, 321
Quercus, 35
  macrocarpa, 552, 578
  Muehlenbergii, 552, 578
  prinoides, 524
  velutina, 504
querula, Zonotrichia, 163, 170, 187, 189, 192, 194, 353, 603
quinquefolia, Parthenocissus, 554
Quiscalus,
  quiscula, 348
  versicolor, 348
quiscula, Quiscalus, 348

rabida, Lycosa, 262
raccoon, 402, 598
racer, blue, 39, 401, 453, 596
racerunner, 39, 444, 466, 469
radicans, Rhus, 554
ragweed, 495, 496, 554
rails, 321-322
Rainey, Dennis G., Eastern woodrat, Neotoma floridana: natural history and ecology, 535
Rainey, Dennis G., and Henry S. Fitch, Ecological observations on the woodrat, Neotoma floridana, 501
rainfall, correlation with reproduction of voles, 384, 385
Rallus,
  elegans, 321
  limicola, 322
Rana,
  catesbeiana, 302, 435
  clamitans, 436
  pipiens, 302, 436, 473
rattlesnake, 469
  timber, 39, 401, 511, 514, 596
Rattus norvegicus, 512
ravens, 336
recovery from injury, collared lizard, 244
Recurvirostra americana, 326
Red
  Crossbill, 163, 170, 171, 172, 350
  fox, 402, 599
  haw, 578
  milk snake, 515
  Phalarope, 326
Red-backed Sandpiper, 325
Red-bellied Woodpecker, 332
Red-breasted Merganser, 317
  Nuthatch, 337
redbud, 552, 573
Red-eyed Towhee, 163, 164, 170, 177, 178, 179, 180, 181, 182, 187, 350
  Vireo, 163, 168, 170, 174, 184, 342
Redhead, 315
Red-headed Woodpecker, 332
Red-necked Grebe, 310
Redpoll, 349
Red-shafted Flicker, 332
Red-shouldered Hawk, 133, 318, 402
Red-tailed Hawk, 133, 318, 401, 402, 597
Red-throated Loon, 310
reduction of population, woodrat, 505
Red-wing, 347
regalis, Buteo, 319
Regulus,
  satrapa, 340
  calendula, 340
Reithrodontomys, 637
  megalotis, 134, 372, 404
reproduction,
  collared lizard, 229
  of voles, correlation with rainfall, 384, 385
  prairie vole, 383
  wood rat, 604
reticulatus, Crotaphytus, 216
Retinella electrina, 121, 124
Rhus,
  aromatica, 551, 568, 573
  glabra, 554, 568
  radicans, 554
  trilobata, 220, 503
Rhynchophanes mccownii, 353
richardsonii,
  Contopus richardsonii, 335
  Falco columbarius, 320
Richmondena cardinalis, 163, 170, 187, 189, 191, 192, 193, 194, 348, 603
Richmondeninae, 160, 207
ricinus, Ixodes, 139
Ring-billed Gull, 327
Ringed-necked
  Duck, 316
  Pheasant, 321
  snake, 39, 455, 469, 603
Riparia riparia, 335
  riparia, Riparia riparia, 335
Rissa tridactyla, 328
roach, 124
Road-runner, 329
Robin, 339
Rock
  Dove, 328
  Wren, 338
roosts, crow, 483
Rosa,
  arkansana, 554
  setigera, 368
rose, 554
Roseate Spoonbill, 313
Rose-breasted Grosbeak, 348, 603
Ross Goose, 314
rossii, Chen, 314
rothschildi, Fregata magnificens, 311

Rough-legged Hawk, 319
Rough-winged Swallow, 335
ruber, Phoenicopterus, 313
rubescens, Anthus spinoletta, 340
rubida,
  Neotoma, 541, 613
  Oxyura jamaicensis, 317
rubiginosa, Dendroica petechia, 343
rubra,
  Piranga, 163, 170, 183, 184, 187, 189, 200
  Piranga rubra, 348
rubripes, Anas, 314
Rubus argutus, 368
Ruby-crowned Kinglet, 340
Ruby-throated Hummingbird, 331
Ruddy
  Duck, 317
  Turnstone, 323
rufa, Calidris canutus, 325
Ruffed Grouse, 320
ruficapilla, Vermivora ruficapilla, 343
ruficeps, Aimophila, 351
ruficollis,
  Hydranassa tricolor, 312
  Stelgidopteryx, 335
Rufous-crowned Sparrow, 351
rufum, Toxostoma rufum, 338
runways and nests, prairie vole, 398
rustica, Hirundo, 335
rusticolus, Falco, 320
Rusty Blackbird, 347
ruticilla, Setophaga ruticilla, 346

Sabine Gull, 328
sabini, Xema sabini, 328
Sage Thrasher, 338
sagrei, Anolis, 253
salicicola, Hylocichla fuscescens, 339
Salpinctes obsoletus, 338
Sanderling, 326
Sandhill Crane, 321
sandpipers, 323-326
sandwichensis, Passerculus, 350
sanitation, woodrat, 587
Sassafras, 34
sativa, Cannabis, 554
satrapa, Regulus satrapa, 340
savanna, Passerculus sandwichensis, 350
Savannah Sparrow, 350
savannarum, Ammodramus, 350
Saw-whet Owl, 330
Say Phoebe, 334
saya, Sayornis saya, 334
Sayornis,
  phoebe, 334
  saya, 334
  yukonensis, 334
scalaris, Dendrocopos, 333
Scaled Quail, 321
Scalopus aquaticus, 133, 407
scandens,
  Celastrus, 524, 554, 568, 578
  Polygonum, 578
scandiaca, Nyctea, 330
scarabaeid, 487, 488, 493, 494
Scardafella inca, 329
Scarlet Tanager, 348
Sceloporus, 259
  occidentalis, 253
  olivaceus, 253
  undulatus, 115, 136, 253
Scincella, 35, 120
Scissor-tailed Flycatcher, 333
Sciurus niger, 603
scolopaceus, Limnodromus, 325
scottii, Aimophila ruficeps, 351
Screech Owl, 330, 401
Scrub Jay, 336
seasonal occurrence, five-lined skink, 41
Seitz filter, 186
Seiurus,
  aurocapillus, 345
  cinereus, 345
  motacilla, 163, 170, 345
  notabilis, 345
  noveboracensis, 345
Semipalmated
  Plover, 323
  Sandpiper, 325
semipalmatus,
  Catoptrophorus semipalmatus, 324
  Charadrius hiaticula, 323
sennetti, Chordeiles minor, 331
senses, woodrat, 586
septentrionalis,
  Anas cyanoptera, 315
  Eumeces, 19, 77, 91, 452
  Parus atricapillus, 337
Sequoia, 34
sequoiensis, Hylocichla guttata, 339
Serology, 159, 185
serpentina, Chelydra, 437
serrator, Mergus serrator, 317
serripennis, Stelgidopteryx ruficollis, 335
serum
  anti-Estrilda, 196
  anti-Junco, 196
  anti-Piranga, 196
  anti-Richmondena, 195, 196
  anti-Spinus, 196
  anti-Spiza, 196-197
Setaria, 371
setigera, Rosa, 368
Setophaga,
  ruticilla, 346
  tricolora, 346
setosa, Euschöngastia, 593
sexdentatus, Orchopeas, 591
sexlineatus, Cnemidophorus, 122, 259, 445

sexual cycle, five-lined skink, 44
Sharp-shinned Hawk, 318
Sharp-tailed
  Grouse, 321
  Sparrow, 351
Short-billed
  Dowitcher, 325
  Marsh Wren, 338
Short-eared Owl, 330
short-tailed shrew, 402, 515, 604
Shoveller, 315
shrew, short-tailed, 402, 515, 604
shrikes, 341
Sialia,
  currucoides, 340
  mexicana, 339
  sialis, 339
  sialis, Sialia sialis, 339
Sigmodon hispidus, 368
Silphium laciniatum, 554
silvestris, Meleagris gallopavo, 321
sinuatus, Corvus corax, 336
sipedon, Natrix, 302, 452
sirtalis, Thamnophis, 302, 453
sitkensis, Loxia curvirostra, 350
Sitta,
  canadensis, 337
  carolinensis, 337
  cookei, 337
  nelsoni, 337
size, prairie vole, 388
s. johnannis, Buteo lagopus, 319
skiltonianus, Eumeces, 77, 91
skink,
  brown, 446
  five-lined, 446, 466, 469, 602
  foot, 7
  Great Plains, 466, 469, 603
  osteoderm, 9
  prairie, 469
  regeneration of tail, 94
  Sonoran, 39
  tail, 8, 94
  tongue, 9
skunk,
  spotted, 402, 511, 512, 596
  striped, 402
Slate-colored Junco, 163, 170, 187, 189, 194, 200, 352
slender tantilla, 39
smalli, Neotoma floridana, 541
Smilax, 34
  herbacea, 524
Smith Longspur, 353
smithsonianus, Larus argentatus, 327
smooth sumac, 554, 568
snail, 115, 484, 493, 494, 495, 602
snake, 484, 496
  brown, 458, 515
  bull, 39, 462, 469, 596
  De Kay's, 447, 453, 466, 469
  garter, 453, 466
snake—*Concluded*
  glass, 444
  king, 39, 462, 515
  lined, 454, 469
  milk, 515
  pilot black, 39, 401, 461, 511, 513, 515, 596
  prairie rat, 469
  ring-necked, 39, 455, 469, 603
  slender tantilla, 39
  water, 452
  worm, 457, 467
snakeroot, 554, 568
snapping turtle, 437
Snow
  Bunting, 354
  Goose, 314
Snow-on-the-mountain, 554
Snowy
  Egret, 311
  Owl, 330
  Plover, 323
social releaser, 50
Solanum, 364, 371
  carolinense, 367, 578
  nigrum, 554, 578
Solidago, 554, 578
solitaria, Tringa solitaria, 324
solitarius, Vireo solitarius, 342
Solitary
  Vireo, 341
  Sandpiper, 324
Somateria,
  mollissima, 316
  spectabilis, 316
  v. nigra, 316
Song Sparrow, 353, 603
Sonoran skink, 39
sonorana, Dendroica petechia, 343
Sora, 322
sorghum, 484, 485, 492, 494, 495, 496, 578
Sparrow Hawk, 264, 320
sparrows, 348-354
sparverius,
  Falco, 264, 320
  Falco sparverius, 320
Spatula clypeata, 315
spectabilis, Somateria, 316
Speotyto,
  cunicularia, 330
  hypugea, 330
Sphyrapicus,
  nuchalis, 332
  thyroideus, 333
  varius, 332
spider, 260, 602
spiderwort, 220
Spilogale
  interrupta, 136
  putorius, 402, 511, 512, 591, 596
spinoletta, Anthus, 340

Spinus, 167
  pinus, 349
  tristis, 163, 170, 171, 172, 187, 192, 194, 350
Spiraea, 34
Spiza americana, 161, 163, 183, 187, 189, 191, 193, 194, 200, 206, 349
Spizella,
  arborea, 163, 170, 187, 352
  arenacea, 352
  arizonae, 352
  breweri, 352
  ochracea, 352
  pallida, 352
  passerina, 352
  pusilla, 352, 603
sponsa, Aix, 315
spotted
  king snake, 515
  Sandpiper, 324
  skunk, 402, 596
Sprague Pipit, 340
spragueii, Anthus, 340
spurge, 487, 492, 494, 495, 496
spurius, Icterus, 347
squamata, Callipepla, 321
Squatarola squatarola, 323
squatarola, Squatarola, 323
Squirrel,
  fox, 604
  gray, 604
Stallcup, William B., Myology and serology of the Avian Family Fringillidae, a taxonomic study, 160
stansburiana, Uta, 259
Starling, 341
Steganopus tricolor, 326
Stelgidopteryx,
  ruficollis, 335
  serripennis, 335
stellaris, Cistothorus platensis, 338
stellata, Gavia, 310
Steller Jay, 336
stelleri, Cyanocitta, 336
Stellula calliope, 331
Stenotrema leai, 602
Stercorarius,
  longicaudus, 327
  parasiticus, 327
  pomarinus, 327
Sterna,
  albifrons, 328
  athalassos, 328
  forsteri, 328
  hirundo, 328
Stilt Sandpiper, 325
stimsonii, Eumeces, 11, 12
Storeria, 120, 122
  dekayi, 453
streatori, Neotoma fuscipes, 613
strepera, Anas, 315
striata, Dendroica, 344
striatus, Accipiter, 318
stricklandi, Loxia curvirostra, 350
stricta, Vernonia, 367
strigatus, Chondestes grammacus, 351
striped skunk, 402
Strix,
  georgica, 330
  varia, 330
Strobilops labyrinthica, 121
Sturnella,
  argutula, 346
  magna, 346
  neglecta, 347
Sturnus vulgaris, 341
subis, Progne subis, 336
subruficollis, Tryngites, 326
succession, 502
sulcirostris, Crotophaga sulcirostris, 330
sumac, 503
  fragrant, 220, 551, 568
  smooth, 554, 568
Summer Tanager, 163, 170, 183, 184, 187, 189, 200, 348
sunflower, 484, 486, 492, 494, 495, 496, 554
Surf Scoter, 317
surinamensis, Childonias, niger, 328
Surnia ulula, 330
Swainson Hawk, 319
swainsoni,
  Buteo, 264, 319
  Hylocichla ustulata, 339
swallows, 335-336
Swallow-tailed Kite, 318
Swamp Sparrow, 353
swans, 313
swenki, Otus asio, 330
swift, 331
Sycamore Warbler, 344
Sylvilagus floridanus, 407, 604
Symphoricarpos, orbiculatus, 368, 552, 554, 578
symplectus, Dendrocopos scalaris, 333

tabida, Grus canadensis, 321
Tachycineta thalassina, 335
taeniatus, Masticophis, 264
Taiga Biome, 29
tail,
  of skink, 8, 94
  regeneration in collared lizard, 244
  regeneration in skink, 94
tamdaoensis, Eumeces, 11, 12
tanager-finches, 161
tanagers, 348
Taraxacum erythrospermum, 367
Taxodium, 34, 35
taylori, Colinus virginianus, 321

Telmatodytes,
  dissaëptus, 338
  palustris, 338
temperature relations,
  ant-eating frog, 282
  collared lizard, 224
  five-lined skink, 18
  woodrat, 555
temperature responses in free-living amphibians and reptiles of northeastern Kansas, 419
Tennessee Warbler, 342
tenuirostris, Charadrius alexandrinus, 323
tephrocotis, Leucosticte, 163, 170, 171, 172, 183
terns, 328
Terrapene ornata, 438, 602
territoriality,
  collared lizard, 250
  woodrat, 521
Tertiary, 11, 33, 34, 35
testes, five-lined skink, 45
teter, Cathartes aura, 317
Teucrium canadense, 367
texensis, Gastrophryne, 278
thalassina, Tachycineta, 335
Thamnophis sirtalis, 302, 453
thapsus, Verbascum, 554
Theridion tepidariorum, 26
thermoregulation, 26
thistle, 578
thrashers, 338
Thraupidae, 161, 207
Thraupinae, 207
thrushes, 339, 340
Thryomanes,
  bewickii, 338
  cryptus, 338
  niceae, 338
Thryothorus ludovicianus, 338
Thuja, 35
thula, Leocophoyx thula, 312
thyroideus, Sphyrapicus, 333
thysanuran, 115
tickle grass, 524
tigrina, Dendroica, 343
tigris, Cnemidophorus, 259
timber rattlesnake, 39, 401, 469, 511, 514, 596
toad,
  American, 423, 469
  garden, 426
  tree, 428
tolmiei, Oporornis, 345
tongue, of skink, 9
Tordoff, Harrison B., Check-list of the birds of Kansas, 309
Totanus,
  flavipes, 325
  melanoleucus, 325
towhees, 350
Townsend
  Solitaire, 340
  Warbler, 344
townsendi,
  Dendroica, 344
  Myadestes townsendi, 340
Toxostoma,
  longicauda, 338
  rufum, 338, 603
Tradescantia, 220
  bracteata, 367
traillii, Empidonax traillii, 334
traps, live, 364, 540
Tree
  Sparrow, 163, 170, 187, 352
  Swallow, 335
  toad, 428
treganzai, Ardea herodias, 311
triacanthos, Gleditsia, 368, 524, 551, 578
triangulum, Lampropeltis, 133, 136, 462, 515
trichas, Geothlypis, 345
Trichuris muris, 588
tricolor,
  Hydranassa, 312
  Steganopus, 326
tricolora, Setophaga ruticilla, 346
tridactyla, Rissa, 328
trifida, Ambrosia, 367
trilobata, Rhus, 503
Tringa,
  cinnamomea, 324
  solitaria, 324
Triodia flava, 367, 397
tristis,
  Anasa, 602
  Spinus, 163, 170, 171, 172, 187, 192, 194
  Spinus tristis, 350
Triticum aestivum, 578
Troglodytes,
  aëdon, 337
  hiemalis, 337
  parkmanii, 337
  troglodytes, 337
troglodytes, Troglodytes, 337
Trombicula
  alfreddugési, 138, 267, 592
  cynos, 592
  gurneyi, 138
  lipovskyana, 267, 592
  lipovskyi, 592
  splendens, 138
  sylvilagi, 592
  trisetica, 592
Tropidoclonion lineatum, 454, 473
Trumpeter Swan, 313
Tryngites subruficollis, 326
Tsuga, 35
Tufted Titmouse, 337, 603
tunganus, Eumeces, 11, 12, 33

Turdus,
  achrusterus, 339
  migratorius, 339
  propinquus, 339
Turkey, 321
  Vulture, 317
Turtle,
  box, 438, 602
  snapping, 437
Tympanuchus,
  cupido, 320
  pallidicinctus, 320
  pinnatus, 320
Tyto,
  alba, 330
  pratincola, 330
Tyrannus,
  tryannus, 333
  verticalis, 333
  vociferans, 333
tyrannus, Tyrannus, 333
Ulmus, 34
  americana, 552
ultramarina, Aphelocoma, 336
ulula, Surnia, 330
umbellus, Bonasa umbellus, 320
undulatum, Cirsium, 578
undulatus, Sceloporus, 115, 136, 253
unicinctus, Parabuteo, 319
University of Kansas Natural History Reservation, 39, 127, 215, 251, 277, 279, 363, 419, 501, 508, 539
Upland Plover, 324
Urocyon cinereoargenteus, 599
usta, Gastrophryne, 279
ustulata, Hylocichla, 339
Uta stansburiana, 259

valeriae, Haldea, 458
valisineria, Aythya, 316
varia,
  Mniotilta, 342
  Strix varia, 330
variabilis, Dermacentor, 594
Varied Thrush, 339
varius, Sphyrapicus varius, 332
vasifer, Herpyllus, 602
Veery, 339
velox, Accipiter striatus, 318
velutina, Quercus, 504
venusta, Neotoma albigula, 613
Verbascum thapsus, 554
Verbena, 364, 371
Vermivora
  celata, 343
  chrysoptera, 342
  orestera, 343
  peregrina, 342
  pinus, 342
  ruficapilla, 343
  virginiae, 343
vermivorus, Helmitheros, 342
Vernonia, 364
  Baldwini, 367, 554
  stricta, 367
versicolor,
  Hyla, 428, 473
  Quiscalus quiscula, 348
Vesper Sparrow, 351
vespertina,
  Hesperiphona, 163, 170, 171, 172
  Hesperiphona vespertina, 349
verticalis, Tyrannus, 333
Viduinae, 207
villosus, Dendrocopos villosus, 333
violacea,
  Nyctanassa violacea, 312
  Oxalis, 367
Violet-green Swallow, 335
virens,
  Contopus, 335
  Dendroica virens, 344
  Icteria virens, 346
Vireo,
  atricapillus, 341
  bellii, 341
  flavifrons, 341
  gilvus, 342
  griseus, 341
  noveboracensis, 341
  olivaceus, 163, 168, 170, 174, 184, 342
  philadelphicus, 342
  plumbeus, 342
  solitarius, 341
vireos, 160, 341-342
virescens,
  Butorides virescens, 312
  Empidonax, 334
virgatum, Panicum, 367
Virginia
  creeper, 554
  Rail, 322
  Warbler, 343
virginiae, Vermivora, 343
virginiana Didelphis, 597
virginianus,
  Bubo, 402, 596
  Bubo virginianus, 330
  Colinus, virginianus, 321
virginicus, Andropogon, 367
Vitis, vulpina, 578
vittatum, Leiobunum, 121, 602
v. nigra, Somateria mollissima, 316
vociferans, Tyrannus vociferans, 333
vociferus,
  Caprimulgus vociferus, 331
  Charadrius vociferus, 323
vole, Prairie, 281, 363
vulgaris, Sturnus vulgaris, 341
Vulpes fulva, 402, 599
vulpina, Vitis, 578
vultures, 317-318

walnut, 39
warbler, 342-346
Warbling Vireo, 342
wardi, Ardea herodias, 311
Waring blender, 186
warreni, Neotoma, 613
wasp, 124
Water Pipit, 340
water snake, 452
Water-turkey, 311
waxwings, 340
weasel, 133, 596
weight, woodrat, 543
wenmanni, Epitedia, 591
Western
  Flycatcher, 334
  Grebe, 310
  Kingbird, 333
  Meadowlark, 347
  Sandpiper, 326
  Tanager, 348
  Wood Pewee, 335
wheat, 484, 485, 492, 494, 495, 496, 578
Whip-poor-will, 331
Whistling Swan, 313
White Pelican, 311
White-breasted Nuthatch, 337
White-crowned Sparrow, 353
White-eyed Vireo, 341
White-faced Glossy Ibis, 313
White-footed mouse, 583, 604
White-fronted Goose, 314
White-necked Raven, 336
White-rumped Sandpiper, 325
White-throated Sparrow, 353
White-winged
  Crossbill, 350
  Junco, 352
  Scoter, 317
Whooping Crane, 321
wild licorice, 554
Willet, 324
Williamson Sapsucker, 333
Wilson
  Phalarope, 326
  Snipe, 324
  Warbler, 346
wilsoni, Bohmiella, 588
Wilsonia,
  canadensis, 346
  citrina, 346
  pileolata, 346
  pusilla, 346
wilsonianus, Asio otus, 330
Winter Wren, 337
Wisconsinan, 30
wislizenii, Gambelia, 227
Wood
  Duck, 315
  Ibis, 312
  Thrush, 339
woodchuck, 604
woodhousei, Bufo, 426
woodhouseii, Aphelocoma coerulescens, 336
woodpeckers, 331-333
woodrat, 501, 535, 613
  behavior, 583
  breeding, 526, 605, 607
  color, 543
  commensals, 515, 601
  communication, 585
  competitors, 601
  development, 604, 616
  ecology, 501, 535
  escape reactions, 599
  food habits, 524
  gait, 545
  growth, 527, 616
  habitat, 502, 545
  heat relations, 555
  homeostasis, 637
  home range, 517
  houses, 560
  life history, 535
  light relations, 559
  litter size and number, 609
  longevity, 530
  measurements, 542
  moisture requirements, 555
  movements, 623
  natural enemies, 511
  parasites, 588
  parturition, 614
  pelage, 587, 621
  population, 623, 631
  posture, 544
  predation on, 511
  reduction of population, 505
  reproduction, 604
  sanitation, 587
  senses, 586
  territoriality, 521
  weight, 543
  young, 615, 620
worm snake, 457, 467
Worm-eating Warbler, 342
wrens, 337-338
Wright Flycatcher, 334

xanthi, Eumeces, 11, 12
Xanthocephalus xanthocephalus, 347
xanthocephalus, Xanthocephalus, 347
Xema sabini, 328
Xysticus elegans, 602

Yellow
  Rail, 322
  Warbler, 343
Yellow-bellied
  Flycatcher, 334
  Sapsucker, 332
Yellow-billed Cuckoo, 329
Yellow-breasted Chat, 346

Yellow-crowned Night Heron, 312
Yellow-headed Blackbird, 347
Yellow-shafted Flicker, 331
Yellow-throat, 345
Yellow-throated Vireo, 341
young, of woodrat, 615, 620
yukonensis, Sayornis saya, 334

Zapus hudsonius, 407, 604
Zea Mays, 578
zebra, Centurus carolinus, 332
Zelkova, 35
Zenaidura macroura, 329, 603
Zonotrichia
  albicollis, 187, 192, 353
  gambelii, 353
  leucophrys, 353
  querula, 163 170, 187, 189, 192, 194, 353, 603

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(Continued from inside of front cover)

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Index. Pp. 647-676.

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(Continued on outside of back cover)

(Continued from inside of back cover)

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Index. Pp. 625-651.

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