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By
Henry S. Fitch

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A Demographic Study of the Ringneck Snake (Diadophis punctatus) in Kansas

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ABSTRACT

Field records of more than 14,000 individuals of *Diadophis punctatus* were assembled over a 26-year period on several small study areas at the University of Kansas Natural History Reservation, mostly within a half-mile radius, with emphasis on marking and recapture. Emergence from hibernation begins in late March and continues into early April, ovulation occurs in the latter half of May, and the elongate, sausage-shaped eggs, averaging approximately 3.9 per clutch, are laid in late June or early July. Hatching occurs at the end of August or in September. Females become sexually mature after their third hibernation, typically at a snout-vent (S-V) length of approximately 235 mm, but males mature a year earlier, at a minimum length (S-V) of 166 mm. Growth continues, but at a reduced rate, after attainment of sexual maturity. Snakes already above average adult size typically gain from one to three per cent in length annually. Mortality of adults is not age-specific, and loss is approximately 25 per cent annually. A small percentage of the snakes survives to an age of 15 or more years. Young seem more secretive than adults and are less well represented in samples.

Sex-ratio in samples is subject to drastic seasonal fluctuation; females range from 24 per cent in early fall to 71 per cent in midsummer, but in late March, April and early May, when the snakes are most in evidence, males are always more numerous. The snakes are active over a wide range of temperatures but tend to maintain body temperatures between 25 and 29.5 degrees C. Their surface activity is chiefly at air temperature within or below this range, and at higher air temperatures they retreat underground. Body temperature is maintained by contact with sun-warmed objects that the snakes use for shelter. Occasionally, at relatively low air temperatures, the snakes venture into the open and bask in sunshine.

Earthworms, especially *Allolobophora caliginosa,* provide most of the food, and it is estimated that each snake consumes on the average approximately three times its body weight in earthworms annually. Seven calculations of population density (based upon recapture ratios) varied from 719 to 1849 per ha and averaged 1266. Eight kinds of predators on the Reservation were found to eat ringneck snakes, but their toll would account for only part of population regulation. The copperhead, racer and Red-tailed Hawk were the predators in most recorded instances, but moles, mice and birds other than raptors may also be among the important predators. Marked snakes were recaptured at distances of zero to 520 m from the original capture site; however, one-fourth were within 10 m, even after intervals of several years, showing a strong tendency to remain within a home area. Home ranges were often elongate, with maximum axes of approximately 140 m. Ranges tend to be progressively altered through time.

INTRODUCTION

The ringneck snake *(Diadophis punctatus)* is a highly successful transcontinental North American species. Its local populations are adapted to the swampland of subtropical southern Florida, the boreal forest of heavily glaciated areas in northern Michigan and the desert grassland of the southwestern United States. Partly because of retiring or secretive habits, the species is considered rare throughout most of its extensive geographic range. However, in a central area including northeastern Kansas, where my study was made, it is abundant and ecologically prominent.

Soon after field work began on the newly-created University of Kansas Natural History Reservation, the ringneck snake attracted attention as one of the common animals meriting intensive study because of its probable ecological roles as a consumer of invertebrates and as an abundant food source for larger predators. In the ensuing 26 years the species has been allotted more time and effort than any other kind of animal in the many autecological studies carried out on the Reservation.

This small snake has proven to be a difficult subject for field study, despite its great abundance. Individuals ordinarily cannot be observed readily under natural conditions. When uncovered or discovered in the open, they are glimpsed only momentarily, escaping underground or into dense vegetation. The snakes cannot be found for most of the year, including, of course, their hibernation season. But they are also difficult to find in summer, especially in hot and dry weather.

The present study had its inception

in the spring of 1949 when I began taking field notes on ringneck snakes and individually marking those that were captured. In the 1950s the snakes were observed or marked only occasionally, as part of a comprehensive program to study the vertebrates of the Reservation. Several students at different times undertook ecological studies of *Diadophis* in the area: John Hawken (1951-1952), Robert M. Hedrick (1956-1957) and Kenneth Shain (1958-1959). Hawken's and Hedrick's records were mostly from the Rat Ledge area, whereas Shain's were from the vicinity of the Reservation headquarters. Although each of these projects was of short duration, their combined data contributed substantially to my study.

In the spring of 1964 large–scale capture and marking of *Diadophis* was undertaken at Rat Ledge, in the field near Reservation headquarters "House Field," and in "Quarry Field" along the northern edge of the Reservation (Fig. 1). On 24 September 1965 a system was initiated for recording the pattern of pigmentation on the posterior ventrals to supplement the clipping of scales as a means of positive individual identification. In 1966, operations at Rat Ledge were abandoned and field work was concentrated in the House Field and Quarry Field areas, which were close enough that snakes often shifted from one to the other.

The marking program was suspended at the end of May, 1968, but in the spring of 1969 all first-year young captured were group-marked and those considered yearlings were individually marked in an effort to gain more information about the growth of young. In the fall of 1969, and in 1970 through 1974, efforts to capture the snakes were continued; those taken were not marked but were measured, weighed, sexed, and carefully examined for marks made in the period 1958 through 1969. Hence, although procedures and areas have varied somewhat from year to year, my intensive field study extended over an eleven-year period, and was supplemented by 15 years' accumulation of earlier data. Expenditure of so much time and energy on a local population of one species may appear prodigal; yet, the recapture records that were the key to an understanding of ecological relationships and population dynamics totalled only a few hundred, and when these were subdivided into sexes and ages, some samples were inadequately small.

Acknowledgments

Members of my family, Alice Fitch Echelle, Chester W. Fitch, John H. Fitch and Virginia R. Fitch, helped me from time to time, both with the field work and with various stages in the analysis of data. Many persons helped in the search and capture of the snakes; Robert R. Fleet's contribution of many large series was especially outstanding. John Hawken, the late Robert M. Hedrick, and Kenneth Shain each contributed data accumulated from one or more seasons of field work. Donald R. Clark, Robert W. Henderson, Richard L. Lattis, Julian Lee, Michael V. Plummer, Eric Rundquist, and Arnold K. Smith were employed as research assistants at different times, and all contributed substantially. In 1971, 1972, and 1973, while engaged in his own field research on the Reservation, Lattis captured and contributed many ringneck snakes marked in 1969 or before; these long term survivors provided some of the most revealing records of longevity, growth, and population structure. Financial support from the National Science Foundation (6-17084) and from the University of Kansas is gratefully acknowledged.

Materials and Methods

In spring ringneck snakes were found in large numbers beneath flat rocks, especially in open woodland or at woodland edge, at hilltop edges including "Skink Ledge," "Rat Ledge," and an old

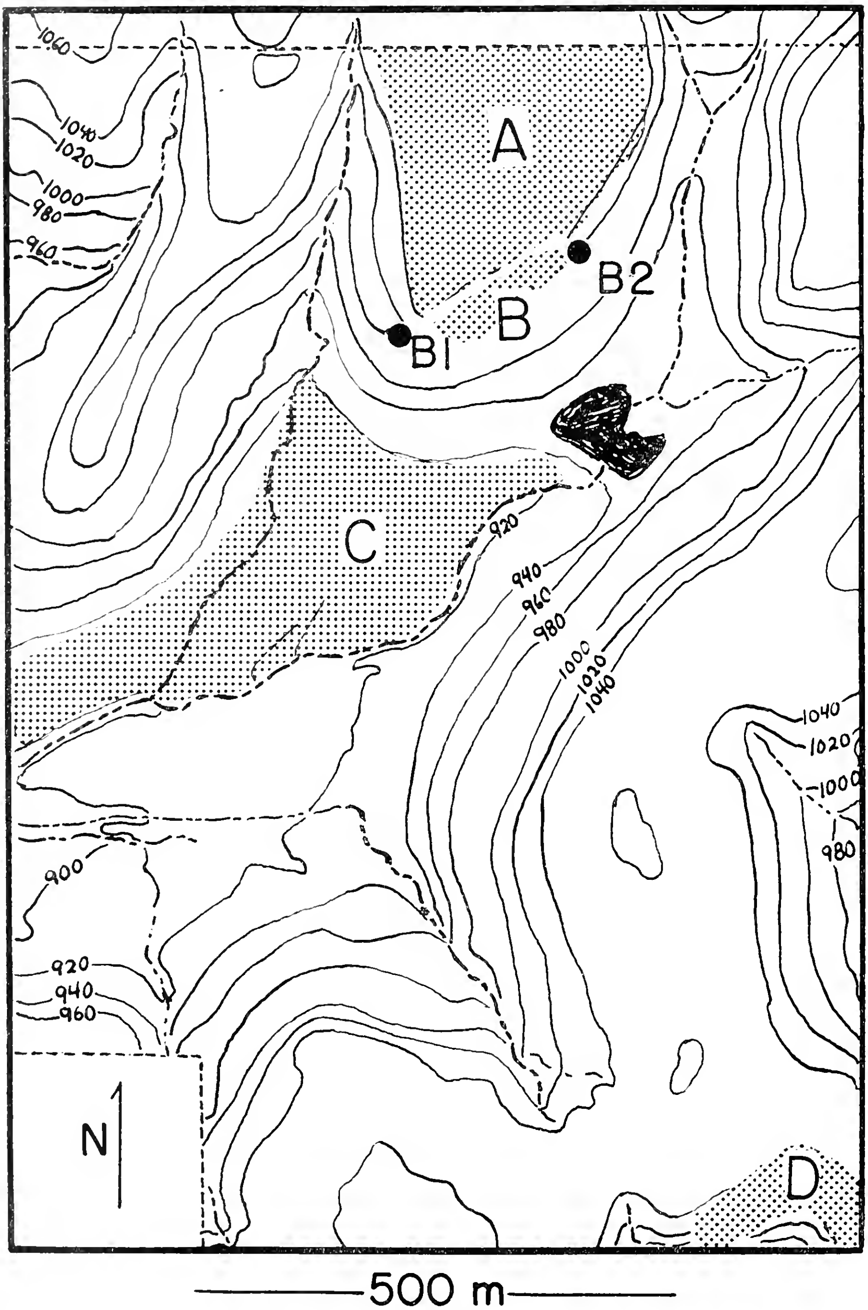

Fig. 1.—Contour map of northwestern part of The University of Kansas Natural History Reservation showing study areas of *Diadophis punctatus*, 1949 to 1974. A. "Quarry Field," a flat hilltop with tall grass interspersed with brush. B. Abandoned limestone quarry at south exposure of hilltop edge. B 1. Hibernation site for snakes from both hilltop and valley, limestone outcrop with southwest exposure. B 2. Egg-laying and "nursery" area at east end of quarry. C. "House Field," at head of small valley. D. "Rat Ledge," limestone outcrops at hilltop edge with south exposure.

rock quarry, where suitable flat rocks were numerous. In 1966 and 1967 funnel traps were used on a large scale. These were adaptations of the cylindrical wire funnel traps used earlier in population studies of larger kinds of snakes at the Reservation (Fitch, 1951; Clark, 1966). A glass quart jar served as the trap body; a funnel of 1/8 inch mesh screen was soldered to the screw-top of the jar. These traps were used in combination with drift fences consisting of strips of sheet metal 2 to 6 m long and 25 to 38 cm wide, buried to a depth of at least 5 cm, so that snakes could not readily pass beneath. A funnel trap was set at each end of the barrier, and traps were generally situated in clumps of grass or other dense vegetation, so that captured animals would not be exposed to direct sunlight.

Strips of sheet metal that were left lying in grassy places from time to time were found to have groups of ringneck snakes congregated beneath them. A series of such experiences brought belated realization that formerly pastured grassy fields harbored high populations of ringneck snakes with densities comparable to those in the rocky upper-slope and hilltop habitats. Subsequently, large numbers of sheet metal strips and weathered boards were distributed over study areas selected in House Field and Quarry Field, and collectively these objects served as highly effective traps. Successful use of these devices as traps depended upon proper timing of field work. The snakes were attracted to the metal chiefly in cool weather, when the metal was warmed by sunshine but air and substrate temperatures were lower than the snake's preferenda. However, at most times the metal was uncomfortably hot or cold to the snakes and was avoided. The boards provided better insulated hiding places and were used at certain times when the metal strips were unattractive. The boards and metal strips proved to be so effective for capture of the snakes that use of funnel traps was discontinued after 1967.

The ringneck snakes captured were processed in the field during the early years of the study, but during most of the study period snakes were brought to the laboratory. Processing consisted of probing for the invaginated hemipenes in the tail base to determine sex and measuring the snout-vent (S-V) length and tail length to the nearest millimeter. For the snout-vent measurement the snake was held against a rigid ruler and gently pulled out straight for several seconds until muscle fatigue caused it to relax momentarily, permitting stretching to the maximum length. The accuracy of measurement was checked in a random sample of 200 adults recaptured within a two-week period—too short an interval for the snake to make measurable growth. Mean deviation from the original measurement was 1.52 mm, approximately 0.6 per cent.

Snakes captured were individually marked by scale-clipping, in a modification of the Blanchard and Finster (1933) system. Three scales were clipped on each snake to attain a unique combination; the left or right end of one of the posterior ventrals was clipped out, also one subcaudal on the left side and one on the right were partly or wholly excised. The subcaudals clipped included numbers 2 to 20 on each side, counting posteriorly from the vent. On each side the count began with the first scale that made contact on or near the midline with a counterpart on the opposite side; smaller scales just behind the vent, which did not extend to the midline, were not included.

Snakes have some capacity to regenerate lost or damaged scales (Conant, 1948) and this capacity seems especially well developed in *Diadophis.* The scars left by clipped scales often became obscure after several years. Regeneration of the scale surface was sometimes so complete that partial fusion along a suture or a break in the sequence of pigmented dots on the subcaudals provided the only clues. Examination of the scars under a dissecting microscope often was necessary before identification was made. Natural scars on the tail were common and were a potential source of confusion. Bites of small predators such as *Blarina brevicauda* caused indentations that sometimes were mistaken for those made by clipping scales with scissors.

Because of these potential sources of confusion or error, it was necessary to supplement scale-clipping with other means of identification. Such means was provided by the variable pigmentation of the ventral surface. Markings on the posterior ventrals (numbers one to ten anterior to the anal plate) were classified as "bars," "blotches," "spots," and "dots" according to their size and shape. The number and position of such marks on each posterior ventral was recorded. In many instances positive identification was based on the ventral markings when it could not have been derived from the scars of clipped scales alone.

Weight was recorded to the nearest one-hundredth of a gram. Laboratory balances were used until 1969 when Oskar Ludi spring scales became available and greatly expedited weighing. Obvious bulges in snakes were palped up to the gullet for identification; and when intact they were removed from the snake for weighing and/or measurement.

Reproductive condition was noted. In females of adolescent size, thickening of the cloaca indicative of sexual maturity was recorded. A drop of normal saline was pipetted into the cloaca, and a smear was taken and examined for motile sperm under magnification x 60. Mature snakes of both sexes often had great quantities of sperm in the cloaca. In the male its presence was considered indicative of breeding condition, and in the female it was considered indicative of recent copulation.

Morphology

Characters of the local population.— The head scutellation is typically colubrine (Fig. 2), with nasal divided, loreal small and rhomboidal, 2 preoculars and 2 postoculars on each side, one anterior and one posterior temporal, and 7 supralabials, the third and fourth in contact with the eye. There are 15 or 17 scale rows, each body scale with an apical pit, anal plate divided; eye with round pupil and golden-brown iris. The following are ratios to snout-vent length in a typical adult male: tail length, 24.50%; head length, 4.38%; body diameter, 2.14%; diameter of eye, .63%; length of longest ventrals, .67%; length of longest dorsals, .56%. The teeth are slender and conical, with the following numbers most frequent on the bones that are dentigerous: dentary 16 (or 17), maxillary (Fig. 4) 13 (or 14), pterygoid 10 (or 9), palatine 20 (or 21). In the dentary series the anteriormost tooth is relatively small and slender, the second less so and the largest are those a little anterior to the middle; farther posteriorly the teeth are progressively smaller and more recurved,

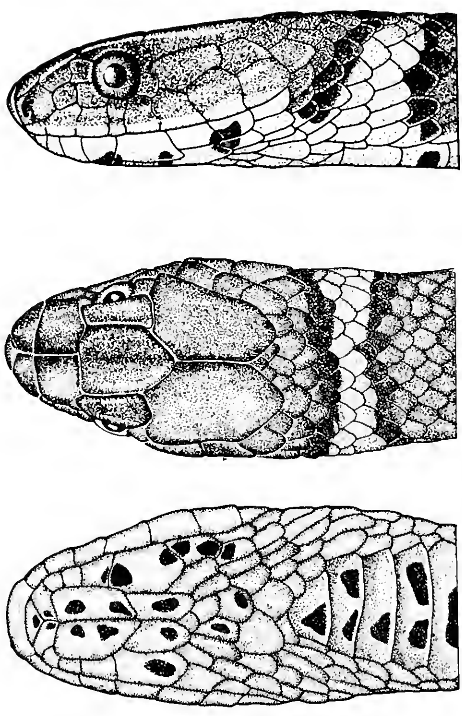

Fig. 2.—Head of adult *Diadophis punctatus arnyi* showing scutellation and pattern; top, lateral; center, dorsal; bottom, ventral.

TABLE 1.—TAIL LENGTH AS PERCENTAGE OF SNOUT-VENT LENGTH IN MALE AND FEMALE RINGNECK SNAKES OF DIFFERENT SIZE CLASSES. FOR EACH OF THE EIGHT SAMPLES $N = 25$.

Size Class	Males	Females
Large adults (*males 298-272 mm, females 347-300 mm*)	22.1 ± .315 (25.4-20.8)	17.9 ± .201 (19.7-15.3)
Typical adults (*males 249-240 mm, females 289-270 mm*)	23.2 ± .323 (25.9-20.7)	17.9 ± .217 (19.8-15.9)
2nd year young (*189-170 mm*)	21.9 ± .069 (23.0-20.9)	17.3 ± .154 (19.1-15.6)
1st year young (*128-111 mm*)	20.8 ± .345 (25.2-17.8)	17.1 ± .248 (18.6-15.4)

with the smallest only about one-third the size of the largest. In the maxillary series the anterior teeth are relatively long, slender and erect, and those farther back are stouter and directed more posteriorly. The last two of the series are almost side by side and are stouter and more backward pointed than the others, and they are separated from the next anterior tooth by a space about equal to the length of that tooth. The palatine teeth are small, about half the size of the maxillary and dentary teeth, with marked decrease in size posteriorly.

Relative tail length is subject to considerable individual variation and also is subject to sexual difference and ontogenetic difference. In 200 randomly selected individuals with intact tails, tail length varied from 15.3 to 25.9% of snout-vent length (Table 1). At all ages males have relatively longer tails, and adults of both sexes have relatively longer tails than do young. In males this ontogenetic change in relative tail length is three times as great as in females. In the largest males the trend is reversed and relative tail length is a little less than in smaller individuals. There is overlapping between the sexes in relative tail length only in the first-year young (12%).

Trends in size, as indicated by snout-vent length and weight, are shown in Table 2. In this table the figures for the largest adult and the smallest sexually mature snake are based upon single individuals, and hatchling size is based upon 83 young of 21 clutches hatched in the laboratory. All other figures are based upon larger samples, with 100 or more snakes in each.

The body color is dark bluish olive dorsally, the head darker than the body. Just behind the head is a pale buffy or dull orange band 1½ scales wide, edged with black both anteriorly and posteri-

TABLE 2.—SIZES OF MALE AND FEMALE RINGNECK SNAKES OF DIFFERENT AGE CLASSES IN A LOCAL POPULATION

	Male		Female	
	Length S-V (mm)	Weight (grams)	Length S-V (mm)	Weight (grams)
Largest adult	315.0	9.0	391.0	----
Average adult	253.6	5.4	281.7	7.0
Young adult (3rd year)	223.0	3.9	243.8	5.0
Smallest sexually mature	168.0	2.0	210.0	3.5
Average 2nd year young (in spring)	184.6	2.3	194.1	2.8
Average 1st year young (in spring)	122.6	.97	127.0	1.05
Hatchling	109.3	.74	114.1	.81

orly. On the side of the head the separation of the darker dorsal color from the paler ventral color is accentuated by an irregular black band along the upper parts of the supralabials. The chin is cream-colored or buffy, speckled with black, and gradually brightening to yellow on the neck and more posteriorly on the ventral surface. The ventral yellow has some orange suffusion which becomes much more prominent on the tail. Black spots are prominent on the ventral surface, and may be arranged in a fairly regular mid-ventral row or may be paired or irregular. Ventrals usually have black areas in their lateral corners. Fig. 3 shows six types of common ventral patterns, but intermediate stages occur, and usually two or more of the types shown are present on the same snake. In a random sample of 200 snakes mid-ventral spots (type A) were most common, with 44.0%, followed by paired spots (types B and C) with 40.7%, blotches and bars (type F) with 6.9%, irregular marks (type D) with 6.0%, and unmarked (type E) 2.4%. The subcaudals have black in the corners and lack other marks.

The hemipenis (Fig. 4) consists of a shaft, and a capitate part which comprises the distal one-fourth. The capitate part is slightly constricted at its base, slightly expanded and shallowly bilobate, with many large and irregular pitlike depressions (calyces). The shaft, except for the part near the sulcus, is covered with spines which are variable in size and distribution and are thick and fleshy except at the tips. The sulcus spermaticus is bifurcate distally.

Geographic variation.—In the population studied, much individual variation was found in characters that have been reported to vary geographically and which are the bases for recognition of the many subspecies of *Diadophis punctatus*. Characters that are notably variable are: body size, dorsal color, ventral color, size and shape and distribution of black markings on ventral surface, presence and width of neck ring, black marking on facial region, number of dorsal scale rows, number of ventrals and sub-

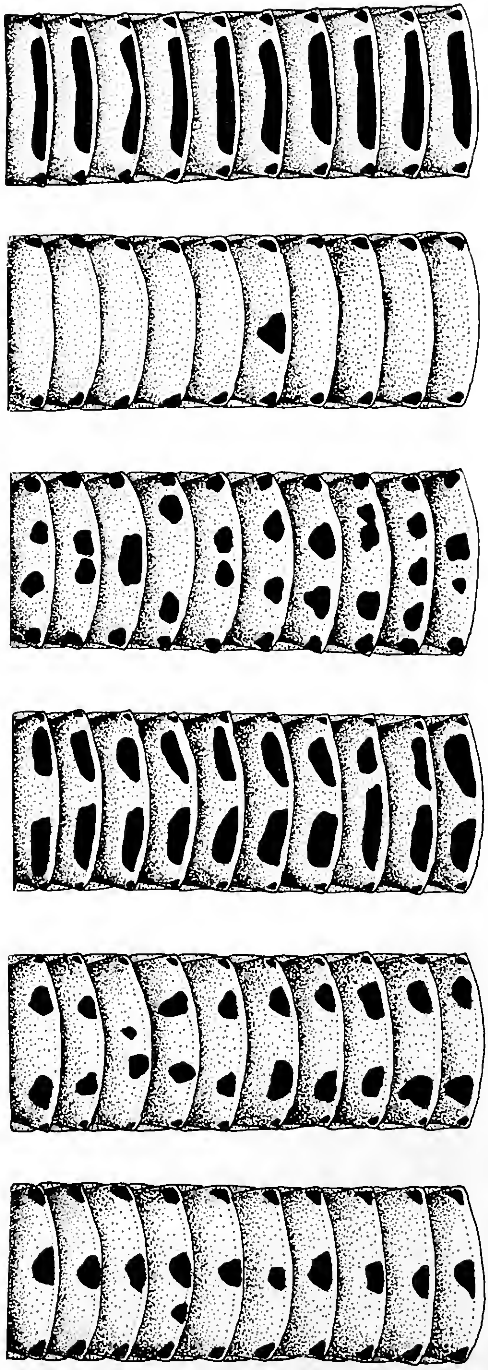

FIG. 3.—Six types of ventral patterns common in ringneck snakes of The University of Kansas Natural History Reservation.

caudals and number of supralabials. The population studied is centrally located in the geographic range of the species, and is intermediate relative to other populations in some of its characters but is near the extreme in some others.

In body size the snakes studied are near the minimum for the species. Populations in the northeastern states, the far West, and especially those in Utah and Arizona, are much larger, up to about twice the linear dimensions of the Kansas snakes. In some regions, especially the far western states, the snakes are more slender than those from Kansas, which appear relatively short and stubby. The dark dorsal color is slaty in some populations but may be suffused with brown, green or blue. In some populations the ventral color is best described as yellow, with relatively little

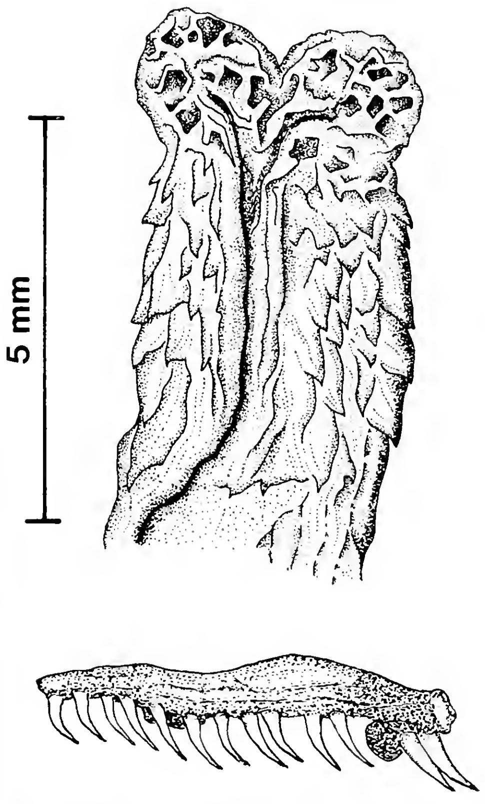

FIG. 4—Above, hemipenis of *Diadophis punctatus;* below, lateral view of left maxillary of *Diadophis punctatus.*

change from body to tail. In others, especially those in which the tail-spiralling response is highly developed, the underside of the tail is coral red. Scales are in 15 or 17 rows in the Kansas snakes and some others. Over much of the range 15 rows are the normal number, but 17 is the normal number in some western populations in which body size is large. In some other western populations which are notably slender-bodied, scale rows vary from 15 to 13. In the population studied, there is normally a neck ring at least 1½ scale rows wide, but in eastern and some far western populations the ring is narrower and/or broken on the middorsal line, and in southwestern populations it is absent. In the Kansas snakes the red or orange ventral color is confined to the ventrals and subcaudals, but in most more western populations the ventral coloration encroaches onto the dorsal scale rows and may cover the first two on each side. The Kansas snakes have seven pairs of supralabials but some other populations have eight. In the Kansas snakes the black marks of the ventral surface tend to be irregular but in the southeastern populations the markings are regular and symmetrical with a half-moon shaped central spot on each ventral scale, and in some far western populations the ventral markings are normally absent.

The number of ventrals in *Diadophis punctatus arnyi* ranges from 142 to 185, and, for the species as a whole, from 126 to 239 (Wright and Wright, 1957:159). The numbers of ventrals in females exceed the numbers in males by from 10 to 20 in different populations. In general, far western populations have more ventrals than *D. p. arnyi* and eastern populations have fewer. The subcaudals number from 30 to 79 and there are usually 6 to 8 more in males than in females within any population.

HABITAT

As a transcontinental species *Diadophis punctatus* occurs in most of the major biomes of North America. In the region of my study it occurs in a variety of habitats but is especially associated with the ecotone between deciduous forest and prairie. Under original conditions the transition from forest to prairie was sharp and clearly defined. Under modern conditions woodlots, groves, old fields and pastures provide a spectrum of combinations of the two main types of vegetation with habitats that are favorable for the snakes.

Ringneck snakes are present on all parts of the Natural History Reservation. However, this area, having a variety of topographic features, past treatments, and plant associations, is unequally used by them (Figs. 5, 6). The transition from low to high numbers reveals the combination of ecological factors required by the species. There is some seasonal shift between habitats, and in some situations where the snakes use loose surface objects for shelter, they are more readily found than where such shelters are lacking, even though the latter situations may have more snakes. Subject to these constraints, habitats represented on the Reservation have been found to have ringneck snakes, in approximately the following order of abundance: (1) Old hilltop pastures dominated by *Bromus inermis*, with thickets, clumps and scattered small trees of *Cornus drummondii, Malus ioensis, Maclura pomifera, Gleditsia triacanthos, Ulmus americanus* and others. Bottomland pastures with similar plant assemblages are slightly less favorable habitat for the snakes, perhaps because they are on the average cooler and damper than the hilltops. (2) Hilltop edges with limestone outcrops and with loose rock strewn over adjacent upper slopes, and with brush and intervening open spaces. South-facing hilltops that are relatively open and have an abundance of flat rocks are preferred over those that face north or are heavily shaded with trees or brush, lack loose ground objects providing hiding places. (3) Woodland; well-drained situations, especially south-facing with an open canopy and little underbrush, are favorable, whereas soggy soil and deep shade under unbroken leaf canopy are unfavorable. (4) Prairie, but generally in association with such features as gullies, rock outcrops and patches of brush, indicating that extensive areas of level, homogeneous grassland are little used. (5) Riparian situations along the edges of intermittent streams or artificial ponds. Especially in dry weather moisture renders these situations attractive, and eroded banks, exposed tree roots, rocks, and accumulations of drift provide hiding places. (6) Old fields, but only after dense ground vegetation has become established, providing shelter.

In summary the snakes are not limited to any one habitat, but occur in various types of terrain and vegetation. Some of the chief requirements are soil that is slightly damp but not wet or soggy, abundant shelter in the form of a surface mat of dead vegetation and/or loose objects such as flat rocks, boards or trash, and screening shrubs or trees with leaf canopies sparse enough to permit abundant sunshine to reach the ground.

BEHAVIOR

Undisturbed ringneck snakes are rarely seen despite their great abundance, because they tend to keep under cover. However, over the 26-year span of my observations at the Reservation, many have been found on a county road that crosses the area or on the driveway between the county road and residence (.5 km). Such a snake, when first seen, was usually motionless and would remain so even when closely approached by a person on foot, or when an automobile passed over it. However, after a pause, especially if actually touched, it would make violent wriggling movements to gain a place of concealment. In a highly excited individual there was sometimes a lateral lashing of the tail as the snake crawled. In all instances the snakes on the road or driveway were

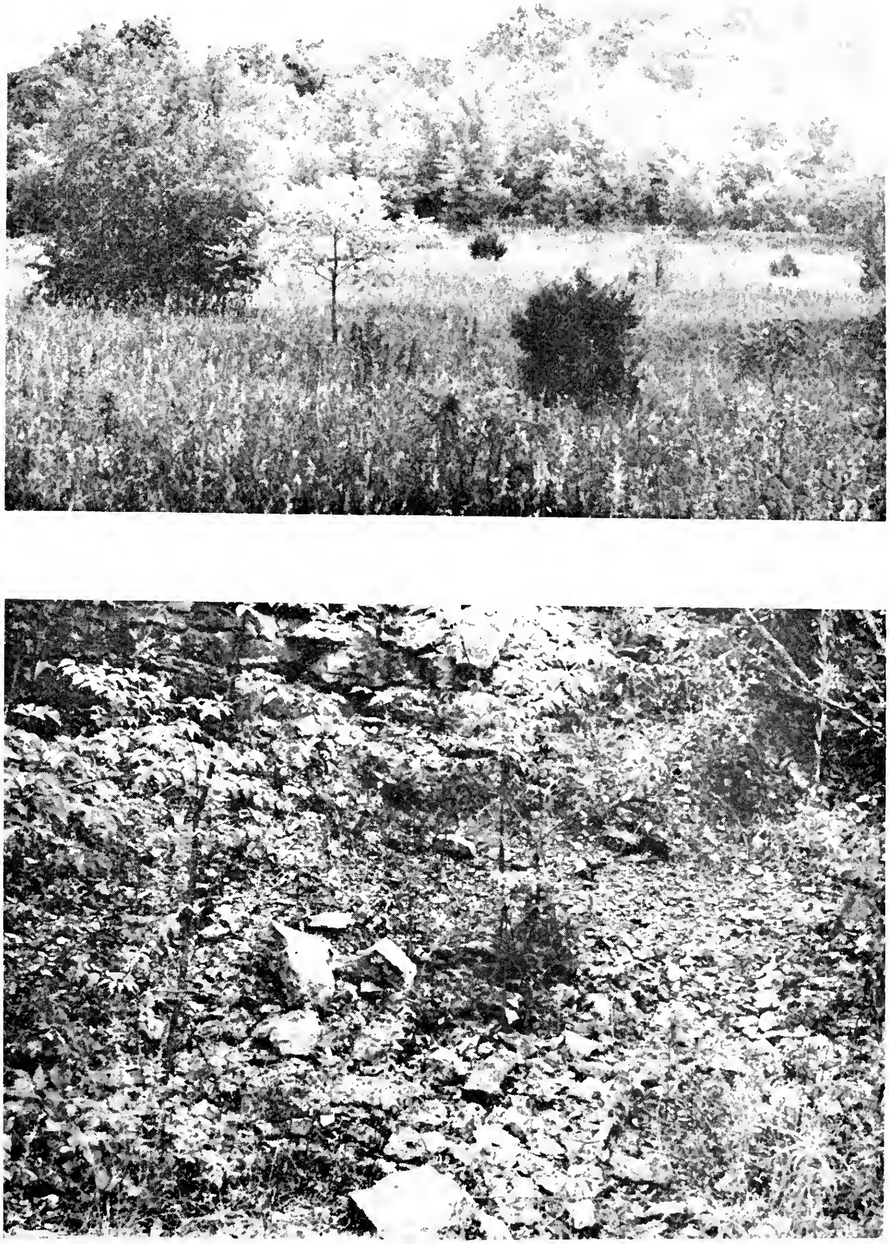

FIG. 5.—Upper, summer habitat of high population of *Diadophis* in "House Field," with dense, low vegetation, scattered trees and brush, July 1974. Lower, nursery area, with sunny, open slope, loose rock, and deep crevices from former blasting, at abandoned quarry where many females congregated for egg-laying; July 1974.

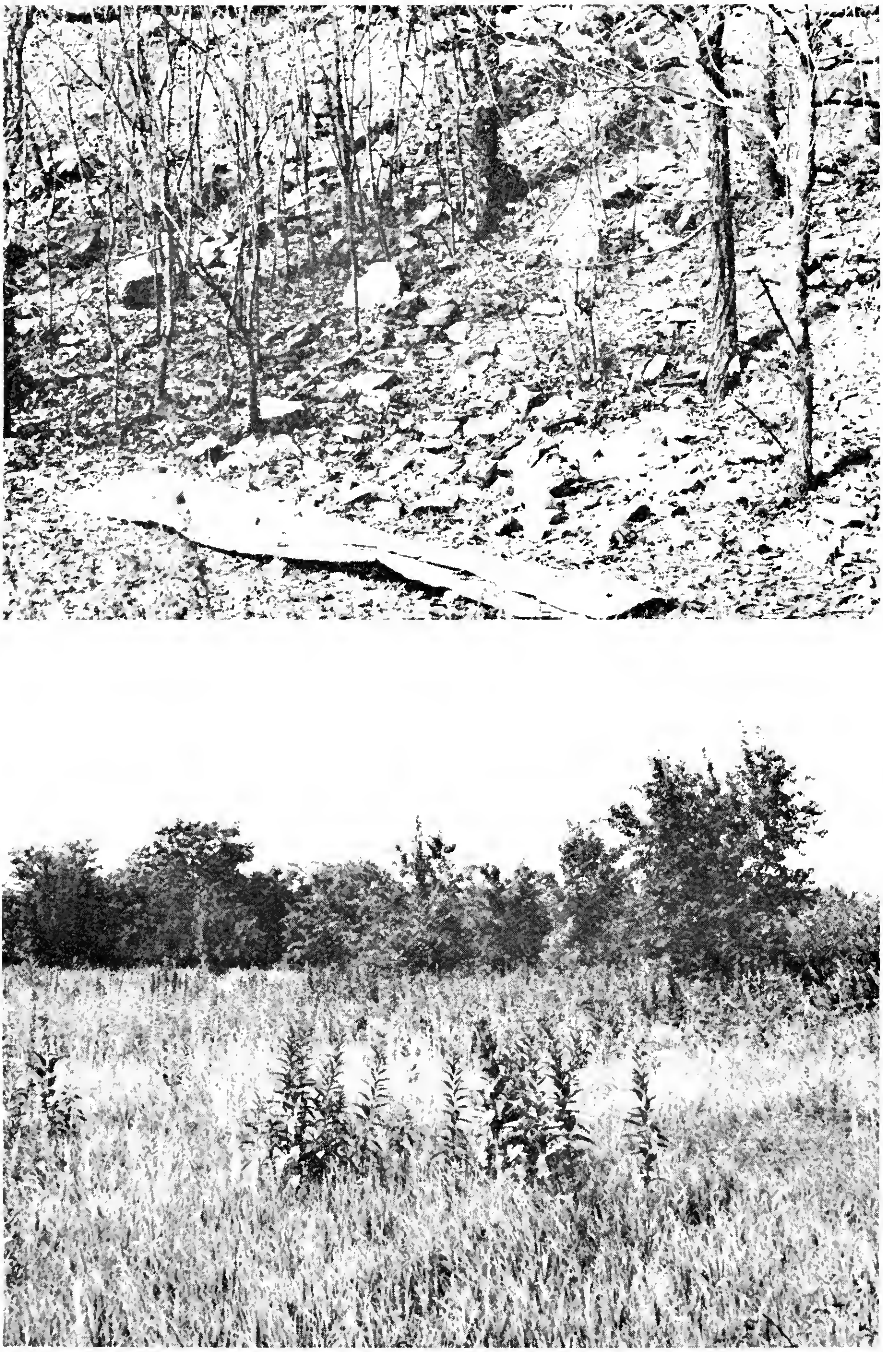

FIG. 6.—Upper, hibernation area at abandoned quarry, with sunny, rock-strewn slope and fissured limestone outcrop in background; metal strip in foreground was attractive to snakes when warmed by sunshine in cool weather; November, 1973. Lower, "Quarry Field," providing optimum summer habitat for the snakes, with dense herbaceous vegetation, interspersed with trees and clumps of brush.

found by day, sometimes in bright sunlight, leading to the conclusion that they are mainly diurnal; but, because of small size and dark coloration, they would not have been readily detected at night. Ernst (1962) observed nocturnal activity in Maryland.

Behavioral thermoregulation usually involves contacting sunshine-warmed objects rather than exposure to direct sunlight. The snakes use flat rocks, and in altered habitats use boards and metal strips. In a horizontal flat coil, the snake has its dorsal surface in contact with the undersurface of the shelter, and may be warmed to above ambient air temperature. When body temperature is sufficiently raised, the snake withdraws from contact with the sheltering object and nestles in a depression, retreats into a hole or crevice, or leaves the vicinity.

The combination of a dark, almost uniform, somberly colored dorsal surface and a brightly colored ventrum combines the advantage of cryptic coloration with the capacity for flashing a startling display, or making a show of sematic colors. Musk with semi-liquid feces and uric acid is voided by a snake that is captured, frightened or injured. A snake struggling to escape writhes vigorously, smearing its captor and its own body with malodorous voided substances. Simultaneously it coils the tail in a tight spiral, elevated so that the coral red undersurface is conspicuously displayed (Figs. 7, 8).

Many genera of snakes, both venomous and non-venomous, have tail displays (Greene, 1973) that may serve to warn natural enemies of venomous or distasteful qualities. However, tail-spiralling is peculiar to *Diadophis*. The display varies in the position of the tail, the number of coils in the spiral, and the kind and degree of stimulation required. Myers (1965) has shown that the response varies geographically, and that it is correlated with intensity of ventral coloring. Those populations in which the ventral surface is all yellow, with no contrast between tail and body, show no spiralling response, or have it only feebly developed. Those populations that have yellow pigmentation of the body grading into bright coral red on the tail have the spiralling response well developed. My own experience has been mostly with *Diadophis punctatus arnyi* of northeastern Kansas, in which the display is relatively well developed, but my limited experience with the subspecies *amabilis* and *occidentalis* in California and Oregon has indicated that in these the response is stronger and more easily triggered than in the Kansas snakes.

At the Reservation in October, 1973, one hundred recently captured ringneck snakes were tested in the laboratory for tail spiralling response. Each in turn was grasped at mid-body with metal tongs, removed from the container where it had been burrowing in decaying wood, and released in a large enamel pan. Grasping the snakes and releasing them in an open place excited them and often evoked spiralling, but if the response did not occur after about five seconds, the snake was tapped on the tip of the snout as further inducement. If the spiralling still did not occur after several taps, the snake was held down against the substrate. If the spiralling did not occur even after several seconds of such restraint, a final stimulus was applied in the form of a light pinch on the rear of the body with sharp-pointed forceps.

When released 12 of the snakes coiled their tails with no further stimulus (in four of these the coil was loose, forming a loop rather than a spiral). Two more coiled their tails when tapped; 46 others did so when held down, but in six of them the tail was merely looped, and in 12 others the spiral was imperfect or loose. Fourteen coiled their tails when pinched (eight of these formed a loop). The remaining 26 snakes did not coil their tails in response to any of the stimuli. However, responses were undoubtedly conditioned somewhat by handling of the snakes in the field at the

FIG. 7.—Upper, adult female ringneck snake and one of her brood of four, illustrating relatively large size of hatchlings; August 1974. Middle, adult female and her clutch of four eggs; July 1974. Lower, clutch of three eggs, one normal (left), one unusually elongate (behind), and one with right angle bend, July 1974.

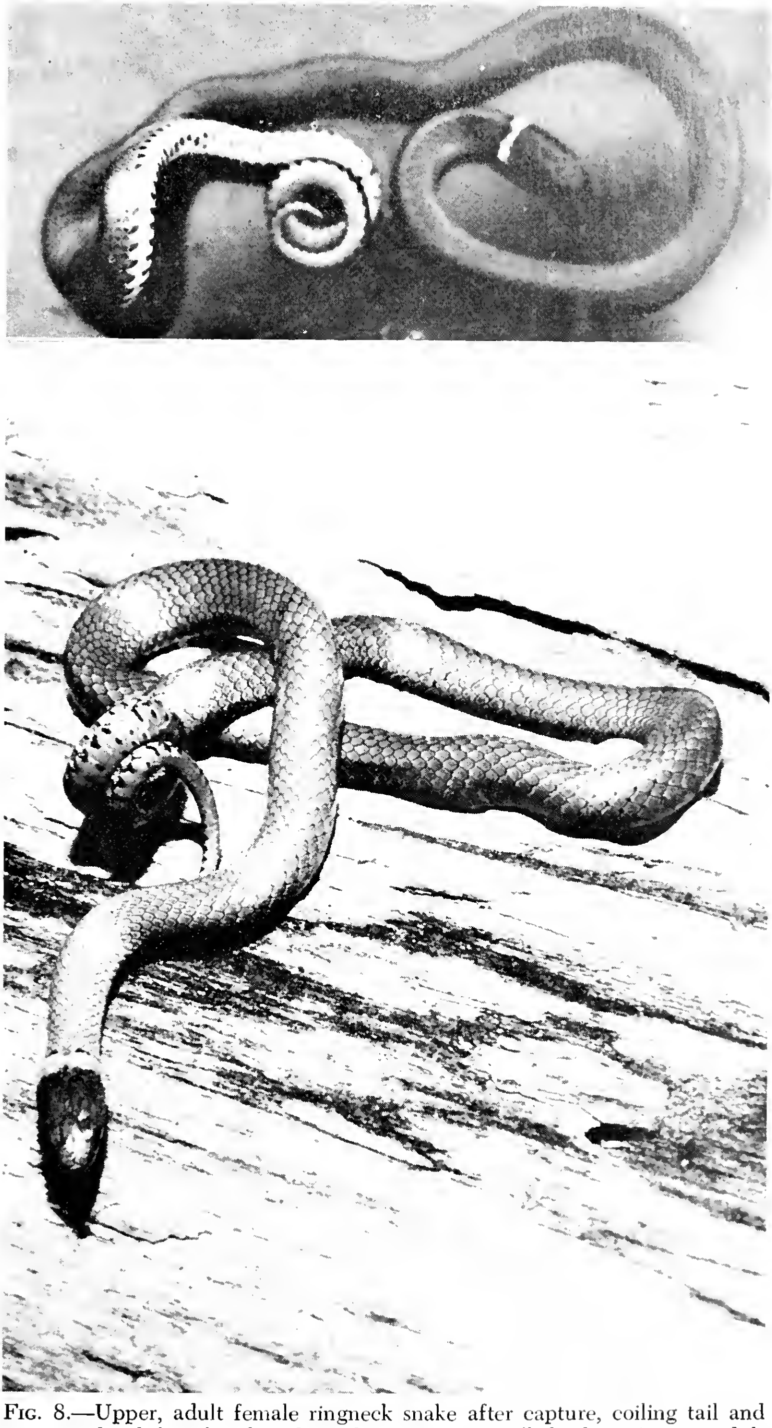

FIG. 8.—Upper, adult female ringneck snake after capture, coiling tail and exposing brightly-colored undersurface in "warning" display. Lower, adult male after handling and release, with tail elevated and coiled in tight spiral displaying bright ventral colors. Photo by Joseph T. Collins.

time of capture, and by repeated stimuli from contact with other snakes when many were in the same container.

In April 1974, 100 more snakes were tested in the field when they were first uncovered, by holding each down momentarily and noting its responses. Ninety-five spiralled their tails, another held its tail in a loop, and only four failed to show any tail coiling. The snakes tested were presumably a random sample and nearly half (48) were adult males. However, the spiralling response seems to be equally well developed in adults and in first year young, and in both sexes.

Tail spiralling is likely to have evolved as a defense against diurnal predators having color vision (especially birds), and the musk is sufficient deterrent to reinforce the display. It may be speculated that in parts of the geographic range where tail spiralling is not developed, other kinds of predators that are nocturnal, or lack color vision, or are not deterred by the musk, are most important.

Although trailing by olfaction is a prominent aspect of the behavior, and ringneck snakes tend to aggregate, social relationships are primitive, and associations between individuals are ephemeral. As in most other snakes, there is no territoriality, and aggressive behavior is rare in intraspecific interactions. However, when many individuals are deposited in the same collecting sack, attacks may occur. In a group of several dozen that have been bagged together, there may be several interlocking pairs, either young or adults and of either sex. In my experience the contestants are always of approximately equal size. The upper individual has the face and muzzle of the lower one in its mouth, while the lower one holds the lower jaw of its opponent, and because of the sharp, recurved teeth, the snakes are not readily disengaged. Anderson (1965) stated that the odor of disgorged earthworms smeared on the snakes' bodies caused them to attack each other, with cannibalism sometimes ensuing. Possibly this is the sole basis for the observed attacks.

TEMPERATURE RELATIONSHIPS

Compared with most other reptiles of northeastern Kansas, the ringneck snake has a relatively long season of activity, averaging about 213 days and excluding only that part of the year in which freezing regularly occurs. Behavorial thermoregulation allows it to maintain a body temperature more nearly optimum than ambient temperatures. Small size and slender habitus permit rapid adjustment of temperature with little effort on the part of the snake.

The snakes occasionally bask in direct sunlight, but usually remain concealed and elevate body temperatures by contact with sun-warmed objects, such as flat rocks, logs, strips of bark, leaf litter, and mats of dead herbaceous vegetation. Artificial objects, including boards, scraps of sheet metal, plastic or tarpaper, are often preferred. The snake lies with its dorsal surface in contact with the overlying object.

Body temperatures averaged 26.1° (11.7° to 34.4°) for 129 snakes found beneath surface objects. In 109 instances body temperature exceeded air temperature and the difference ranged from zero to 13.6°. Only nine per cent of the snakes (11) had body temperatures that were lower than nearby air temperatures. For 37 snakes found in the open, body temperature averaged 26.6° $\pm$ .62 (18.2° to 33.3°). Air temperatures ranged from 16.2° to 30.0° at the times these snakes were found, and for the entire group body temperature averaged 3.7° above air temperature. Only four of the 37 were cooler than the air.

When air temperature approaches or exceeds their preferendum, the snakes tend to stay under shelter, but when air temperature is relatively low, the opportunity to bask in sunshine provides incentive for them to move into the open. For instance on 20 April 1955, when air

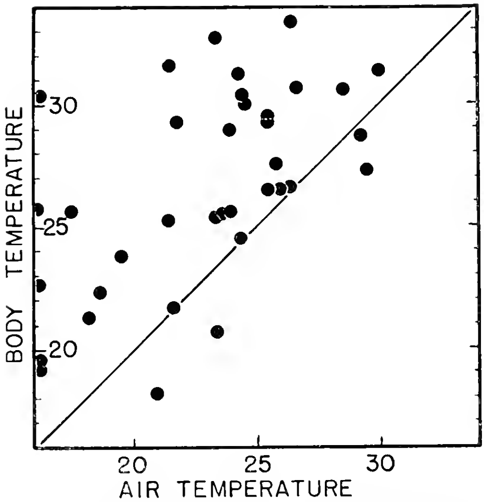

FIG. 9.—Body temperatures of *Diadophis punctatus* and adjacent air temperatures (degrees Celsius), in snakes found in the open. Body temperature is usually a little higher than air temperature and ranges from 19° to 33° in snakes that are active.

temperature was 16.3°, a basking snake had body temperature of 30.3°. Below 16° the snakes do not venture into the open, but still are responsive to vertical temperature gradients, moving upward to contact sun-warmed objects, or downward to escape surface chilling. Figures 9 and 10 show body temperatures and nearby air temperatures for snakes that were in the open and those that were beneath surface objects. The majority of snakes found active on the surface were between 25° and 27° or between 29° and 31°. The majority of those found under shelter had temperatures of 26° to 30°. The highest body temperature, 34.4°, was of a gravid female in June, as were those of several other records exceeding 30°. Seemingly the females while carrying eggs have a strong tendency to bask, and perhaps their preferendum is slightly above that of other individuals.

The maximum body temperature recorded was 34.4°, but the snakes are able to tolerate considerably higher temperatures, at least for brief periods. Experimental exposures demonstrated that for *Diadophis* the critical maximum is approximately 41° and the critical minimum is approximately freezing (Fitch, 1956, 1965). Although the lowest body temperature recorded was 11.7°, it is certain that the snakes tolerate lower temperatures during hibernation. Winter temperatures in hibernacula from .3 to .8 m beneath the surface are usually well within the range 0° to 10°.

SEASONAL SCHEDULE

On the Reservation ringneck snakes have been found in every month except January and February, and only one has been observed in December. Ordinarily the snakes become active in the third or fourth week of March and retire to hibernation in late October or early November. Some emerge later and retire earlier. Even those that are potentially active may be immobilized for days at a time near the beginning and ending of their season of activity when weather is inclement.

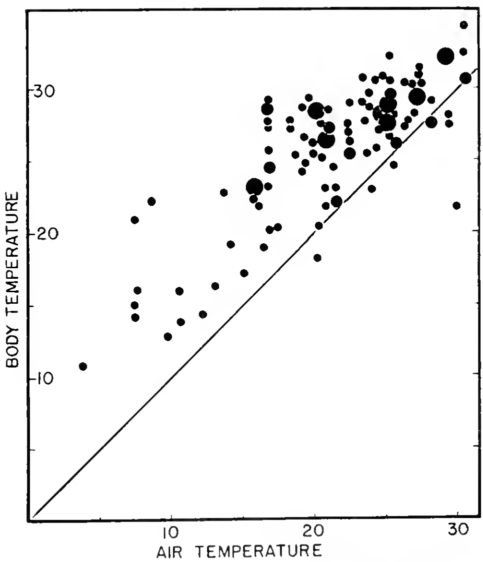

FIG. 10.—Body temperature of *Diadophis punctatus* and adjacent air temperatures (degrees Celsius), in snakes found under shelter. Largest circles each represent three records, medium circles each represent two, and smallest circles each represent one. Body temperatures are concentrated at 25° and 30°.

Probably some individuals remain in the areas where they have been active and hibernate in such shelters as are available there, including the tunnels of voles *(Microtus)*, moles *(Scalopus)* and probably cicada nymphs *(Tibicen, Magicicada)*. Others make trips of hundreds of meters to hilltop rock outcrops where there are deep crevices that provide more secure hibernacula. Emergence from hibernation in spring occurs over several weeks and is controlled by temperature that depends not only on weather but on the location and depth of the hibernaculum. Fall retirement into hibernation also spans several weeks for the population as a whole, judging from the dwindling numbers of snakes found active in late October and early November.

Adult males seem to emerge somewhat earlier than females; anyhow they are much more in evidence at first. There is a shift from rock outcrops to more open situations during April, and some shuffling of populations occurs as individuals that have hibernated together scatter and mingle with individuals from relatively remote hibernation sites. Ovarian follicles, minute at the time of emergence from hibernation, enlarge rapidly in early May, and ovulation takes place in late May or June. Sloughing occurs in most of the population in late April or early May. Beginning in early May the snakes become increasingly secretive and subterranean, and by midsummer they are rarely found. Egglaying occurs in late June or early July, and hatching in the last week of August or in September. Also in September a combination of cooling weather and heavy rains cause the snakes to reappear in abundance in superficial situations where they have not been in evidence since spring. In late September and October there are population shifts back to the vicinity of hibernacula.

Table 3 shows an incomplete phenology for ringneck snakes on the Reservation. The first tabular row shows both mean dates for various events in the annual cycle and mean sizes (length S-V) of first-year young. The subsequent rows are for specific years and show deviations in days from the mean date, or deviation in millimeters from the mean length.

ASSOCIATED ANIMALS

On the Reservation and nearby areas in northeastern Kansas many species of animals are associated with the ringneck snake, and elsewhere in its geographic range the snake interacts with other, quite different communities. In the area of my study, earthworms were the animals most important in its ecology, providing its main food source. *Allolobophora caliginosa* is much more important than all other kinds combined, in terms both of the frequency with which *Diadophis* interacts with it and the biomass of food that it provides. This is a medium-sized, stubby-bodied, tan-colored earthworm that is native in Europe (Dr. W. Murchie, pers. comm.) and introduced into North America, where it is now widespread and abundant, occurring in various habitats. It is especially abundant in damp soil under flat rocks in open woodland or woodland edge in the same sorts of situations that are favored by the snakes.

Other associated animals may be grouped roughly into those that affect the ringneck snake indirectly by extensive alteration of the general habitat, those that prey upon it, those that are potential competitors for food, those that themselves are potential food sources, and those that are essentially neutral in the ecology of the snake. In the first category are livestock (mainly cattle) and deer, which alter the vegetation and soil by their feeding, trampling and droppings. They may often kill snakes by accidental trampling. Also, they may improve the habitat by removing dense vegetation and creating open areas where the snakes have more opportunity to bask. Areas that are subjected to

TABLE 3.—PHENOLOGY OF *Diadophis punctatus* AT THE UNIVERSITY OF KANSAS NATURAL HISTORY RESERVATION OVER A 22-YEAR PERIOD.

						S-V lenth of Young				
	Earliest recorded activity	Earliest recorded female	Last gravid ♀	First spent ♀	First hatchling	Late Sept.[1]	Early Apr.[2]	Late Apr.[3]	Early May[4]	Late May[5]
Yearly Mean	27 Mch.	31 Mch.	7 Jul.	26 Jun.	3 Sep.	127.4	124mm	129mm	132.4mm	136.4mm
Yearly Deviation From Mean										
1952	−26				− 2					
1953	+ 7	+11								
1954	− 1								− 6.0	−2.1
1955	+23	− 5				−1.6				
1956	0	+ 4							+11.0	
1957	+11	−20						− 5.6	− 5.0	
1958	− 6	− 4	− 6	+7	+ 1	+ .8				
1959	+ 3	+ 1		+4			+ 3.7			
1960	-------		− 0.6				+ 0.8	+ 2.3	− 0.6	
1961	-------		− 5.6			−5.1	-----	+ 2.9	− 5.8	−7.5
1962	-------					+2.8	− 4.8	− 1.2		-----
1963	-------						+12.5	+10.9		-----
1964	− 6	− 2	+ 1.9			+6.0	+ 1.6	+ 2.0	+ 1.9	-----
1965	− 4	− 1			+13	+3.2	+ 6.6	+ 5.0	+ 5.3	+3.0
1966	+ 9	+15	− 4.0	−4	− 5	+3.7	+ 2.4	+ 1.9	+ 5.4	+1.5
1967	0	+ 4	+11	+4	+ 0		+ 3.2	+ 1.3	+ 1.4	+2.1
1968	+ 1	+ 5	+17	−7	+ 1		+ 8.1	+ 3.1	-----	-----
1969	+ 7	+11	− 2.0	−8	+ 6		− 2.8	− 3.9	+ 7.8	+3.2
1970	+10	− 6	− 7.0	+2	+ 9		− 0.8	− 3.1	0	+0.03
1971	− 3	+ 1					-----	+ 3.1	0	−1.7
1972	+10	+14			+ 0.1		− 2.2	0	− 8.0	−6.3
1973	− 9	− 6					− 4.4	− 2.9	-----	

[1] Hatchlings, N = 445; [2] yearlings, N = 1046; [3] yearlings, N = 710; [4] yearlings, N = 398; [5] yearlings, N = 148.

medium or heavy grazing support higher population densities of the snakes than do ungrazed areas that are otherwise comparable. Small animals that dig extensive burrow systems also alter the habitat by rendering it more favorable for the snakes, which spend much time underground yet lack capacity for digging. The mole *Scalopus aquaticus,* chiefly in woodland, and the vole *Microtus ochrogaster,* chiefly in grassland, provide an abundance of tunnels that are used by the snakes. The mole is the more persistent burrower, but its burrows ordinarily are not open until broken into by larger animals or by running water. The main tunnel systems of both these mammals are horizontal and somewhat less than 10 cm beneath the surface. Burrows of the pocket gopher *Geomys bursarius,* pine vole *Microtus pinetorum,* and bog lemming *Synaptomys cooperi* may also be used. Much more available shelters are the cylindrical, vertical emergence tubes of cicada nymphs *(Tibicen pruinosa, Magicicada septendecim, M. cassini* and others). The tunnels are usually somewhat more than 1 cm in diameter, large enough for the snakes to move and turn in, and provide convenient retreats to depths where moderate temperature and high humidity prevail. Ordinarily the tunnels of the larger *Tibicen* are most available, but in the emergence years of *Magicicada,* such as 1947 and 1964, the soil is riddled with tunnels and the availability of shelters is tremendously increased, especially for small individuals of *Diadophis.*

Known and suspected predators on the snakes are mentioned in the section on predation. Of these predators, the mole and the two species of shrew also feed to a large extent on earthworms and are potential competitors of *Diadophis.* Other earthworm-feeders that might compete with *Diadophis* are mostly small snakes including *Carphophis vermis, Thamnophis sirtalis* (especially first-year young), *Storeria dekayi, Virginia valeriae* and *Tantilla gracilis.* All of these are much more specialized than *Diadophis* in their habitat requirements, but overlap *Diadophis.* None approaches the high population densities attained by *Diadophis,* which is usually the dominant kind even where it occurs in association with one or more of the others.

Tantilla gracilis and *Virginia valeriae* are remarkably small snakes; young or even adults are potential prey for *Diadophis.* In Arizona *Tantilla wilcoxi* has been recorded in the food of *Diadophis* (Van Denburgh, 1922:654). A hatchling *Ophisaurus attenuatus* is the only lizard recorded in the prey on the Reservation, but hatchling skinks *(Eumeces fasciatus* and *Leiolopisma laterale)* are a potential food source, as are newly metamorphosed anurans *Acris crepitans, Pseudacris triseriata, Bufo americanus,* and *Gastrophryne olivacea.*

FOOD HABITS

In my study, made near the center of the species' geographic range, the trend of the food habits differed notably from the trend indicated by published literature, or by any single published account. Significant geographic variation in food is evident, and seems to be correlated with parallel changes in size, bodily proportions, habitat and behavioral traits.

Ernst (1962:266), in a brief popular account based mainly on observations in Maryland, wrote that earthworms, small salamanders (especially *Plethodon cinereus),* slugs, grubs, newborn snakes, toads, frogs and various insects were eaten. He stated, "I have observed ringnecks capturing winged insects that have fluttered to the ground after being attracted to a night light." Myers (1965: 63) obtained stomach contents of 74 of the snakes from Alachua County, Florida; 26 had earthworms, one contained a salamander *(Manculus quadridigitatus),* four contained narrow-mouthed frogs *(Gastrophryne carolinensis),* two had juvenile frogs *(Rana pipiens)* and another contained an unidentified frog, two contained ground skinks *(Leiolopisma laterale)*, and one contained unidentified reptile scales. Myers also recorded a salamander, *Eurycea bislineata*, from the stomach of a ringneck snake from Leon County, Florida. In northern Michigan, Blanchard, Gilreath and Blanchard (in press) found from the combined evidence of food disgorged by captured snakes, and from experimental offering of possible prey species to those in confinement, that the salamander *Plethodon cinereus* was preferred and was preyed upon much more often than any other species, although earthworms and hatchling snakes were also taken.

At Big Black Mountain in eastern Kentucky, Barbour (1950:104) obtained a sample of ringneck snakes *(Diadophis punctatus edwardsi)* and dissected 53, 18 of which contained prey. It consisted chiefly of the salamanders, *Plethodon glutinosus, Desmognathus fuscus* (both adults and larvae), *Eurycea bislineata* and *Aneides aeneus* (eggs). However, wood roaches were 11.1% in frequency and 7.5% in volume. Other insect fragments and miscellaneous debris were interpreted as stomach contents of the salamanders.

Gehlbach (1974:144) stated that in Texas ringneck snakes (both *D. p. arnyi* and *D. p. regalis*) feed mainly on small reptiles. In laboratory tests he found that they would catch and hold small snakes such as *Virginia* and *Sonora* and would chew or cling to the site of the original bite, sometimes for several hours, until the prey was immobilized, seemingly killed or paralyzed by the toxic saliva, conducted into the wound by the enlarged posterior maxillary teeth.

Most earlier literature was summarized by Wright and Wright (1957) who discussed food habits separately for each of nine kinds of *Diadophis* currently considered conspecific, but recognized as valid subspecies. They are *amabilis, modestus, occidentalis* and *similis* of the West Coast, *edwardsi* and *punctatus* of the eastern United States, *laetus* and *regalis* of the arid Southwest and *arnyi* of the central states. In discussing their food habits Wright and Wright cited the publications of 28 earlier authors. In most instances the food records for each kind of ringneck snake were obtained by a different group of authors. Of the nine subspecies figuring in the records, seven were reported to have eaten insects, seven had eaten snakes, five each had eaten lizards, salamanders, frogs and earthworms, two had eaten toads and one had eaten slugs. The subspecies *arnyi*, which includes the population on which my own study is based, had eaten prey of all these categories, excepting slugs.

In summary the literature records indicate that *Diadophis punctatus* is euryphagous; its known food includes diverse types of small terrestrial animals of four phyla. Therefore, it is remarkable that a sample from the Reservation, much larger than any assembled elsewhere, indicates feeding almost entirely limited to one kind of prey. Stomach contents were palped from each of 182 snakes captured on the Reservation in 14 different years from 1951 to 1974. The 224 items included 221 earthworms, two tipulid larvae and one hatchling glass lizard *(Ophisaurus attenuatus)*. Many of the earthworms were identified as *Allolobophora caliginosa*, and probably most were of this species.

A total of 347 fecal droppings were collected from the ringneck snakes processed in 1959, 1960 and 1961, and were examined under a dissecting microscope. In 56 of these "scats" there was nothing identifiable, but in each instance the material seemed to consist mainly or entirely of soil which might have been residual from the digestive tracts of earthworms after the soft parts had been dissolved. In 291 scats some hard parts of the prey remained, providing a clue to its identity; 288 contained only setae of earthworms, three contained fragments of chitin as residue from insect prey, and two contained both setae and chitin fragments. Traces of plant material occurred in 177 scats. Some of this vegetation was still green but most of it was old and decayed; it might have come from the guts of earthworms, or might have been ingested accidentally as the snake swallowed prey.

Miscellaneous materials found in scats included masses of nondescript soft tissue (probably from earthworms in most instances), crystals of uric acid, teeth of the snakes themselves, soil particles, and (in two instances) fine hairs or hairlike fibers.

Each of 170 snakes checked for stomach contents contained one earthworm and nine snakes each contained two earthworms. Probably in many instances the food that happened to be in the stomach was undetected when the snake was processed. The elongate shape of an earthworm usually caused no discernible bulge in the body of the snake. The part of the prey in the posterior end of the snake's stomach disintegrated first, and palpation did not readily reveal presence of the object. In April 1973 special effort was made to detect food in the stomach or fecal material in the hind gut. Of 83 snakes processed on 6, 11, 12, 13, 17 and 18 April, 34 produced scats when the rear end of the body was palped and 17 had stomach contents; 9 of these snakes yielded both stomach contents and scats. Thus 42 of the 83 snakes had food or food residue in the digestive tract.

In 70 instances in which both the snake and its earthworm prey were measured, the worm averaged 34.1 $\pm$ 1.58% (14 to 97) of the snake's length (S-V). In 45 instances in which the intact earthworm was weighed, it averaged 11.9 $\pm$ 0.87% of the snake's weight. Such relatively small prey might be expected from the minute head, delicate jaws, and attenuate body of the snake. Frequency of feeding is no doubt greater in these snakes than in those which ingest relatively bulky prey.

Henderson (1970) performed a series of feeding experiments using snakes from the same population that I studied. Starting with snakes that had empty digestive tracts, he found that the first defecation occurred in as little as seven hours after feeding in snakes maintained near their maximum temperature tolerance, at 35°, and that first defecation ordinarily occurred in from 15 to 30 hours in snakes kept at 24° to 33.° Digestion can occur even at low temperatures; in one snake kept at 7° defecation occurred after 312 hours. Henderson found that after an earthworm meal there were from two to six (average 4.2) successive defecations, with four occurring most frequently. At 33° last defecation occurred only two or three days after ingestion, and at 25° it occurred in four or five days.

Combined evidence of Henderson's study and my own field data suggest that the average ringneck snake feeds about once every eight days, that about half the interval is required to digest and assimilate the meal, and that the snake has an empty digestive tract for the remaining half. At this rate of feeding a snake would take about 27 meals, ingesting approximately three times its body weight, in a normal growing season estimated at 213 days.

SPATIAL RELATIONSHIPS

In the course of routine field work, numerous snakes captured for processing were generally deposited in the same container without noting the precise capture points. For these, distances travelled between captures were usually not known, but, as recapture records accumulated, it became evident that each snake had usually stayed within the same small study area such as the quarry, Quarry Field or House Field. Likelihood of recapture was greater in those that stayed in the study areas than in those that wandered away from them, but spacing of the study areas was well adapted to show relatively long movements, when a snake shifted from one study area to another, and such shifts were recorded occasionally.

Some of the capture records that were obtained involved precise stations such as those occupied by funnel traps at the ends of the drift fences, and pieces of sheet metal put out to attract the snakes. When two or more of the capture records for any individual involved such definite field stations, the distances between them could be readily measured on the map. In all, 433 such measurements were obtained and these averaged 80 m (0 to 1700). In 86 instances the distance was recorded as zero, but the actual capture points may have been as much as several meters apart. Table 4 shows the trend toward greater distances with elapsed time. In general, the longer the time, the farther the snake would be from any given starting point. However, each snake tends to revisit certain points from time to time, and to turn back into a known area instead of wandering indefinitely.

The 433 distances measured include several types of movements such as day-to-day foraging for food, gradual or abrupt shift from one favored area to another, and regular seasonal migrations involving travel to and from hibernacula or egg-laying sites, but in most cases these cannot be distinguished. In order to determine the usual distance of travel between hibernacula and summer ranges, the records of individuals captured in March or October (presumably near the place where hibernation had occurred or would occur) and caught also between late April and mid-September (presumably where they were spending the summer) were examined. Fifty such movements averaged 121 m and half of them were in the range 67 to 174 m. Many other snakes, caught in early April or late September, were probably near their hibernacula and their relatively long movements between these sites and their summer ranges raise the average somewhat.

Figure 11 shows the recorded movements grouped in 10 m intervals. It shows that nearly one fourth of the movements were distances less than 10 m and one third more were between 10 and 70 m and 22 per cent were between 70 and 140 m, with the remainder longer distances up to 1700 m. The histogram reveals a trend toward progressively fewer records for longer distances. There seem to be rather abrupt reductions beyond distances of 10 m, 70 m and 140 m, respectively, and these steps may have biological significance. The much larger number of records between 0 and 10 m than in any other 10 m interval, especially, indicates attachment to small areas. The significance of these many short movements is believed to be, in part, the slow rate of travel of the snakes, so that one recaptured after several days, or perhaps even after several weeks, often would still be lingering in the vicinity of its previous capture, without having covered much of its actual range. Also, habitual return to a favorite spot within the home range, even after long intervals, must have been involved. In many instances a snake was recaptured

TABLE 4.—DISTANCES TRAVELLED BY MARKED AND RECAPTURED RINGNECK SNAKES IN VARIOUS TIME INTERVALS.

	1 to 5 Days	6 to 10 Days	11 to 20 Days	1 Month	2 to 6 Months	7 to 18 Months	More Than 18 Months
Number of Records	46	43	38	38	66	120	69
Average Distance (meters)	80	106	134	250	300	310	447
Range of Distances Travelled (meters)	0 to 820	0 to 444	0 to 600	0 to 700	0 to 1200	0 to 1700	0 to 1550

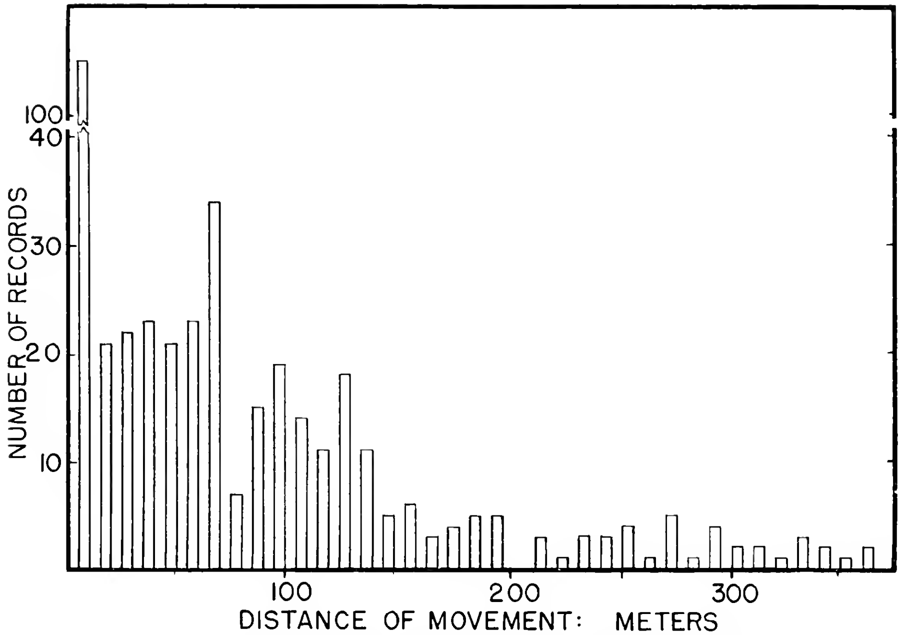

FIG. 11.—Distances moved by individual ringneck snakes between captures.

at approximately the same place after a year or more.

Movements up to 70 m are numerous and their numbers are near the same in each 10-meter interval. These probably represent normal movements within a home range and suggest that a normal home range may have a diameter of approximately 70 m. Between 70 and 140 m, records are less numerous than they are for shorter distances and tend to decrease gradually; beyond 140 m there is an abrupt decrease. It is suggested that the many recorded distances between 70 and 140 m were mostly within the home ranges of the individuals concerned, and that they reflect unusually large or elongate ranges. The relatively few distances exceeding 140 m are probably outside the snakes' normal ranges and represent shifts or extensions of original home range, or perhaps small scale migrations between summer ranges and hibernacula or egg-laying sites.

In other kinds of snakes it has been found that the kind and amount of travel and size of range differs greatly according to the sex and age of the individual. Undoubtedly such differences exist in *Diadophis* also. However, the sample obtained was heavily weighted to adult males (58 per cent) with relatively few adult females (11%) and first-year young (both sexes combined 17%) and even fewer second-year young (both sexes combined 14%). Average distances were 44.4 m for first-year young, 55.0 m for adult males and 102.1 m for adult females. The proportion recaptured at the original location differed significantly: 43.8% in first-year young, 17.7% in adult males and 11.7% in adult females.

The finding that first-year young are much less vagile than adults is in line with what is known about other snakes, and animals in general. It was surprising to find that adult females averaged nearly twice as much distance as adult males, and were relatively seldom recaptured at an original capture site. Probably their greater vagility is correlated with their larger size, and with the fact that at least some of them travel to and from special nesting areas.

REPRODUCTION

Diadophis punctatus is oviparous and its reproduction is on an annual cycle. Ovarian follicles are minute at the time of emergence from hibernation, they enlarge rapidly in late spring, ovulation occurs in June and egg-laying occurs in late June or early July. Incubation is mainly in July and August and hatchlings usually appear near the end of August or in September.

Aggregation and Mating.—Trailing by olfaction brings the sexes together and increases opportunity for mating. Dundee and Miller (1968) showed that the small aggregations of ringneck snakes frequently found under sheltering objects in spring result from following of the scent trail left by contact of the skin with the substrate. When one individual has found a shelter, others may follow it there. Aggregations are most prominent in spring when surface activity is at its peak, but are evident also in fall. Although the snakes are seldom seen in summer, they probably aggregate then, but in deeper and better insulated shelters than are used in spring and fall. The females at least in some instances use communal egg-laying sites.

The aggregations found in spring include both adults and immatures, males and females. There is some tendency for the first-year young to aggregate with others of their size segregated from adults. However, in general adult males make up a high proportion of the individuals in aggregations, which probably form partly as a result of sexual search.

Skin odors are the basis for trailing (Noble and Clausen, 1936; Dundee and Miller, 1968) but it is not clear how much discrimination is exercised by the trailing individual in distinguishing sex and reproductive condition of the one being followed. Musk from the scent glands is secreted only when the snake is frightened or injured, and its odor inhibits trailing.

Sexual behavior is inhibited by capture and handling and unnatural surroundings, and has never been observed in the many ringneck snakes kept in confinement at all times of year. Even under natural conditions sexual behavior has rarely been observed, and this is remarkable in view of the great abundance of the snakes. Active courtship was observed on 24 September 1959 at 4 P.M. The female involved was in process of sloughing and was crawling slowly through the surface litter in open woodland, partly exposed. The slough had peeled back for about half the length of her body. A male was beside her, facing in the opposite direction. For several minutes that the snakes were watched, the male alternately lay passive or made jerky, animated courtship movements, obviously stimulated by scent emanating from the moist, newly-exposed skin. The snakes moved out of sight beneath leaf litter, and when it seemed that they would not reappear, leaves were gently brushed aside exposing the pair to view. Meanwhile another male had joined them and both males pressed against the female but the anterior ends of all three snakes were concealed. Posterior ends of the two males were momentarily intertwined and were apart from the female. There was no evident rivalry between the males as each pursued its courtship, but confusion and delay resulted from the presence of the extra male. Soon the snakes again moved out of sight and could not be relocated.

Copulation was observed at approximately 5 P.M. on 7 May 1974. The pair of snakes was found in damp soil beneath a heavy decaying plank. They did not separate when exposed by turning of the plank nor for about 20 minutes subsequently that they were kept under observation. The female was nervous and active, darting out her tongue almost continually, shifting position frequently, and sometimes crawling a short distance, dragging the relatively passive male after her. From time to time the snakes coiled together in a fairly compact mass, the male often pressing his snout against the female's side. After a few minutes' gap in the observations, the snakes were found to have disappeared and could not be relocated.

Reproductive Cycles.—In four different years on dates representative of the entire season of activity, a total of 484 adult males were tested for motile sperm by gently palpating the rear of the abdomen to eject renal and fecal wastes, then pipetting a drop of physiological saline into the cloaca. By gentle backward massaging of the posterior part of the abdomen, semen was pressed from the vas deferens into the cloaca, and into the droplet of saline solution, which was expressed from the anus onto a glass slide and examined. Active sperm were found in 98.0 per cent in April ($N = 204$), 95.4 per cent in May ($N = 65$), 91.0 per cent in September ($N = 165$), and 93.4 per cent in October ($N = 30$). Of 19 males tested in June, July and August, only one lacked motile sperm. Negative results did not necessarily indicate that sperm were absent; they may have been overlooked. The tests indicate that most adult males have motile sperm throughout the year and that insemination might occur at almost any time, providing males have sexual drive and females are receptive.

In adult females sperm can survive for relatively long periods in vascularized pouches of the oviducts, but probably their maximum survival in the cloaca is only a few days at most. In a few instances tests revealed massive clumps of sperm, but more often the numbers were small, and at all times of year the majority of females tested were negative. The 625 females tested had the following percentages with active sperm in different months of the season of activity: 0 in March ($N = 28$), 5.8 per cent in April ($N = 197$), 20.2 per cent in May ($N = 178$), 16.4 per cent in June ($N = 61$), 0 in July ($N = 30$), 0 in August ($N = 16$), 7.9 per cent in September ($N = 63$), and 2.5 per cent in October ($N = 80$).

On 1 May 1966 seven large females, all negative for cloacal sperm, were dissected. All but one had quantities of active sperm in the oviducts. Ovarian follicles were only beginning to enlarge (largest 6.0 to 8.5 mm, much short of the size at ovulation which is usually 25 mm or more). On 24 April 1955, six females were dissected and they contained an average of 6.5 small ovarian follicles ranging from 1 to 6 mm in length but with a distinct bimodality in size. The larger, clustered about a length of 5 mm, were probably destined for ovulation in the current season, while the smaller clustered about a length of 1 mm, probably would have been retained until the following year.

In May follicles enlarge rapidly and ovulation occurs in June. In eight different years 86 females captured in June, their bodies distended with eggs, were held in confinement until deposition of their clutches. Average egg-laying date for this group was 3 July ($\pm$ .87 day), but dates extended from 19 June to 24 July with a standard deviation of 7.25 days. Much of this variance resulted from the difference between years; egg-laying and other phenological events in the annual cycle of the local population may be accelerated or retarded by unseasonably mild weather or cold weather at critical times in spring.

On 6 August 1965 a female of 319 mm (S-V) was found to have three shelled eggs in her oviducts and the eggs contained living embryos larger (3.3 mm) than those usually found in freshly laid eggs. This date, 34 days later than the average oviposition, indicates a spread of more than six weeks in egg-laying and explains the presence of hatchling sized snakes in late spring when most have grown well beyond this minimum size.

Peterson (1956:152) noted a remarkable instance in which a female *Diadophis punctatus stictogenys* from the Miami area of southern Florida gave birth to a litter of six living young. In this case the eggs were retained in the female beyond the usual time of laying. In newly laid eggs of *Diadophis* the embryos are somewhat more advanced than are those of many other kinds of oviparous snakes.

Eggs.—The eggs are elongate and remarkably variable in shape (see Fig. 7). Often they are nearly cylindrical, but in some the ends tend to be pointed. In some both ends are similar but in others one end is more enlarged. Typically the eggs are somewhat curved, and sausage shaped.

In 251 eggs of 72 clutches, width varied from 21.7 to 46.8 per cent of length. The length averaged 25.2 ± .277 mm (17 to 43). Width averaged 7.11 ± .045 mm (5.2 to 10.0). Weight averaged .89 ± .001 grams (.58 to 1.35).

The eggs are white, but the soft, thin shells are partly translucent so that the coloring of the yolk is faintly visible. The eggs are firm and turgid when laid and as incubation proceeds they gradually absorb moisture from the surrounding medium, and eventually they almost double their original weight. As liquid is absorbed, the eggs become increasingly turgid by stretching of the shell, and the shape changes slightly, with more increase in girth than in length.

Besides the eggs of normal appearance, females kept in confinement in late June and early July sometimes laid eggs that lacked shells and were inviable. Often one or more such eggs were laid in a clutch along with normal eggs. The inviable eggs averaged slightly smaller, and are flaccid rather than firm. Clark (1970) in his study of *Carphophis* also found that confined females often produced unshelled eggs, and he concluded "Shell-deposition may be a crucial step in development, such that a gravid female collected and confined prior to shell deposition generally reacts by laying her eggs in their premature condition." In *Diadophis* likewise, eggs that lack normal shells are believed to result from handling and/or confinement of the females at a critical stage in their egg production.

Size of Clutch.—For 300 clutches, mean was 3.89 ± .083, with a range of one to ten. Data were obtained from unlaid eggs, either found in females dissected, or palpated in live individuals, and from eggs laid by females isolated in confinement. Some of the more important factors affecting size of the clutch are size (and/or age) of the female, the year, and the stage of development at which counts are made, since apparently some eggs are eliminated between the time of ovluation and oviposition.

TABLE 5.—NUMBER OF EGGS PER CLUTCH AND RELATIVE PRODUCTIVITY OF FEMALES OF DIFFERENT YEAR CLASSES.

Length (S-V) of Females	Most Probable Year-class of Females	Number of Ovigerous Females in Sample	Mean Number of Eggs	Range	Percentage of Females in Each Year-class	Percentage Eggs Produced by Each Year-class
210*- 256	3rd	50	2.70 ± .160	1-5	26.6	20.0
257 - 272	4th	82	3.23 ± .109	1-6	21.4	19.0
273 - 280	5th	46	3.67 ± .155	2-5	12.1	12.4
281 - 287	6th	25	3.68 ± .208	2-6	8.8	9.0
288 - 294	7th	28	3.93 ± .210	2-6	7.6	8.2
295 - 300	8th	30	4.17 ± .225	2-10	5.1	5.9
301 - 305	9th	12	4.25 ± .392	2-6	4.1	4.8
306 - 310	10th	16	5.06 ± .225	4-7	3.8	5.3
311 or larger	11th or older	50	5.26 ± .310	3-8	10.5	15.4

* Most females that are fecund or have reached their third year are 235 mm or more.

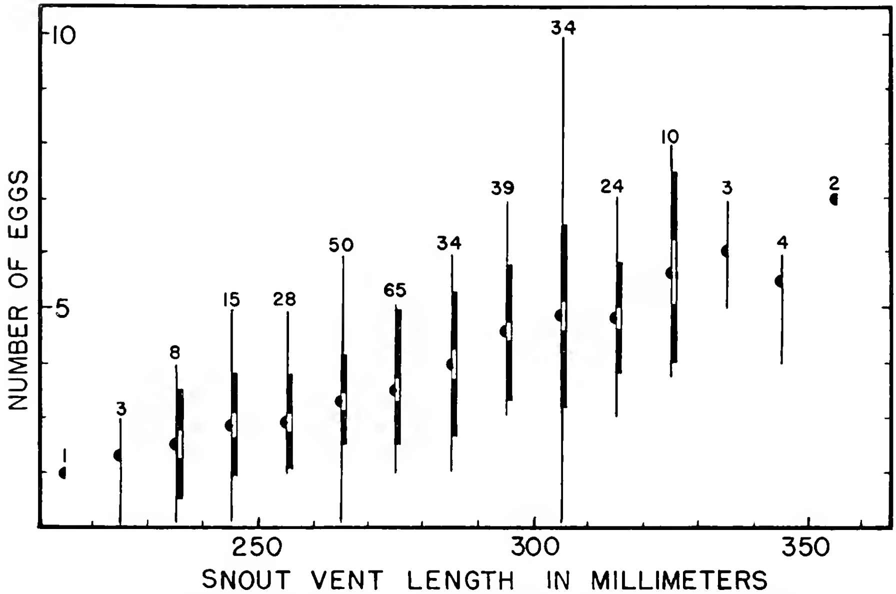

FIG. 12.—Number of eggs per clutch in female ringneck snakes, showing relationship of clutch size to length of female. Mean, standard error, standard deviation and range are shown for each of the larger series.

Eggs laid averaged 3.36 ± .153 per clutch ($N = 50$), whereas those palped or dissected averaged 3.96 ± .096 ($N = 267$). These figures imply that 15 per cent of the eggs are eliminated between ovulation and oviposition. However, most of the records of eggs laid were obtained in 1965 when clutch size may have been smaller than in other years. In 1974, 53 unlaid clutches that were palped averaged 3.81, and 17 clutches that were laid averaged 3.47. All the females that oviposited in captivity had been palped two or three weeks earlier and some loss may have resulted.

In Table 5 females are grouped on the basis of size according to most probable age, and it is shown that the mean size of clutch increases from 2.37 in probable third-year individuals (producing first clutches) to 4.95 in those that are probably seven years old or more. In Figure 12 females are further divided according to length with a 10 mm interval; a steady increase in size of clutch according to size of female is indicated, except that females in the 290-299 mm class averaged higher (4.74) than those in the 300-309 or 310-319 classes (4.33 and 4.65). Seemingly size, as such, rather than age determines productivity.

Table 6 shows mean numbers of eggs per clutch in different years, arranged in order from the largest clutches (in 1963) to the smallest clutches (in 1965), along with weather factors that might be expected to affect fecundity. Amount and distribution of precipitation affect availability of earthworms, which provide most of the food. Ova are minute when the snakes emerge from hibernation in March. Therefore, availability of food in the spring period of April, May and the first half of June might be expected to control the development of eggs, and the availability of earthworms as food would depend on both the amount and distribution of moisture. In Table 6 the number of days having precipitation and the amount of precipitation during the supposedly critical spring period and during the 11½ months preceding the time of ovulation are shown. There is no evident correlation. In a study of *Car-*

TABLE 6.—FECUNDITY AND WEATHER.

Mean Number of Eggs Per Clutch	Year	Days With Rain, April, May, Early June	Precipitation April, May, Early June	Precipitation July Through Early June
5.15 (N=14)	1963	23	180	897
4.70 (N=17)	1962	18	168	956
4.43 (N=14)	1961	25	281	946
4.23 (N=30)	1966	25	280	827
4.00 (N=14)	1973	18	231	1340
3.97 (N=60)	1969	16	326	1070
3.83 (N=12)	1960	21	236	922
3.75 (N=60)	1974	27	273	1195
3.43 (N=51)	1970	23	396	900
3.23 (N=23)	1965	25	405	1117

phophis vermis in the same general area, Clark (1970) found seemingly significant correlation between precipitation and size of clutch. Like *Diadophis, Carphophis* is an earthworm eater.

Reproductive Effort.—The amount of energy and material used in producing eggs or young and the frequency of such reproductive effort differs greatly in different kinds of snakes. Also it differs intraspecifically, according to the age and size of the female (Fig. 13). More information is now available for *Diadophis punctatus* than for any other kind of snake.

In 248 eggs of 71 clutches, weight of egg averaged 0.890 ± .01 gram, and eggs that seemed normal varied from 0.58 to 1.35 gram. Clutches averaged 3.89 eggs, hence average clutch-weight is calculated to be 3.47 grams.

Most typical adult female weights can be obtained at the end of the growing season when females are not gravid and those that produced clutches in early summer have had time to recuperate. In a composite September sample from 1965, 1966 and 1969, average weight of adult females was 4.26 ± .11 grams (N = 72). From these samples it is calculated that weight of the newly-laid clutch averages 81.4 per cent of the non-breeding weight of females.

Lower ratios of weight of clutch to weight of snake were obtained by weighing individual gravid females that were almost ready to lay, then reweighing them and their newly-laid clutches separately. In a series of 52 females, clutch-weight was 39.4 ± .88 per cent of pre-laying weight. Clutches ranged from 20.8 to 51.1 per cent of pre-laying weight of snake. To determine whether reproductive effort was affected by size of female, the sample was divided among large (S-V 295-340, N = 19), medium

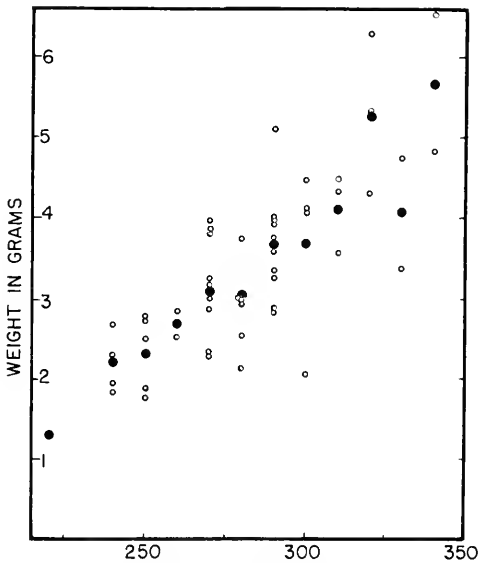

FIG. 13.—Weight of clutch in relation to length of female; solid circles show means and small, open circles show individual records.

(S-V 275-294, $N = 12$) and small (S-V 225-274, $N = 21$) females. Clutch-weight (as percentage of snake-weight) differed as follows in these three groups: large, 40.9 ± 1.10 per cent; medium, 39.1 ± 1.69 per cent; small, 38.1 ± 1.67 per cent. These figures suggest that reproductive effort is greater in larger females than in smaller, but the difference is relatively small.

Even with equal reproductive effort the larger females produce more eggs than the smaller. Table 5 shows the quota of eggs calculated for each annual age group. It shows that because of their relatively large numbers third year females produce the most eggs (one-fifth of the total), despite their relatively low individual productivity. Because of declining numbers, successively older age groups produce slightly fewer eggs, although individually the snakes become more productive.

Nests.—Eggs were rarely found under natural conditions, and most of those observed were obtained from gravid females held in confinement. However, on several occasions eggs were found in natural nests in damp soil beneath large, sunken flat rocks. At the Reservation headquarters on 3 August 1970, a communal nest was found by workmen tearing down a brick structure enclosing an electric water pump. The brick wall was cracked and crumbling as a result of weathering; 15 eggs, probably representing four clutches, were found in the cracks. These eggs were partly incubated and the females had left the area.

Probably communal nesting is the rule, judging from the fact that large concentrations of hatchlings were found year after year at certain favored spots. Such concentrations were found in September, October and even April; meanwhile, hatchlings were relatively scarce in the areas where most adults were found. The 93 snakes obtained 1-15 April 1973 were from three locations, each showing a characteristic biased ratio of hatchlings to adults (and second-year young) as follows: nesting area at east end of quarry ($N = 40$), hatchlings 78%; rocky upper slope near hibernacula at "Tomb Rock" 165 m southwest of first location ($N = 28$), no hatchlings; "House Field" ($N = 25$), hatchlings 16%.

The nesting area at the east end of the quarry was the best known one, and it must have been used by dozens of females from the adjacent field, judging from the numbers of hatchlings found. The actual nests were not found, as search for them would have damaged the habitat. Numerous potential nest sites were provided by niches and deep crevices in the limestone outcrop shattered by quarrying operations, with blasting, more than 25 years before, and by the rock-strewn slope below it. A second nesting area was near the middle of the old quarry, approximately 60 m southwest of the first and perhaps not entirely distinct from it. Two other important nesting areas were known at Rat Ledge.

These nesting areas were all situated along hilltop outcrops of the Oread Limestone, in relatively open situations of southward exposure. Another nesting area was in bottomland approximately 245 m west and a little south of the Reservation headquarters, where the driveway crossed a gully. An old and weathered stone check-dam, a cracked concrete slab, and a rock fill provided shelters with favorably moist nesting sites, but there was some risk of flooding when the gully filled with run-off water after unusually heavy rains.

Although hatchlings tend to be concentrated in preferred nesting areas, many others that seem to be recently emerged are scattered in open habitats where the adults spend most of their time. Probably some of the females find nest sites without shifting from the areas where they live. Abandoned burrows such as those of prairie voles and cicadas are abundant in the snakes' habitat, are often used by the snakes, and on occasion may serve for egg-laying sites.

GROWTH

Growth was studied by (1) direct measurement of gains in length and weight of individuals marked and recaptured, and (2) average differences in length and weight between series in discrete annual age groups. Both methods are fallible and need to be used with caution, and in combination.

The growth in marked individuals is not typical of that in the entire population because these small and delicate snakes are adversely affected by routine processing and fail to grow normally for an indefinite period afterward. Of 55 recaptured after one to ten days, seven had gained weight and 48 had lost with a mean loss for the whole group of 5.44 per cent. In those recaptured after 11 to 20 days five had gained weight and 17 had lost with a mean loss for all of 5.36 per cent. In 21 to 30 days four of another group had gained weight and 13 had lost with mean loss of 11.1 per cent. Of 18 caught in spring and recaptured in fall after intervals of 139 to 197 days, 12 had gained and six had lost with a mean average gain of 8.4 per cent. Each sample consisted of different individuals and all were fully adult so that growth in length had stopped or greatly slowed. From these records it can be concluded that the deleterious stunting effects continue to be severe as much as a month after handling, but that by four to six months these effects have largely worn off. The direct cause of stunting is not definitely known but perhaps handling and processing causes some shock, aggravated by bruising or tearing of delicate tissues when the snake is grasped firmly and stretched to full length for measurement, and results in a period of fasting.

In any one year most eggs are laid within a few days in midsummer and the hatchlings that emerge constitute a cohort which at first is readily distinguishable from older and larger young. However, some of the hatchlings, although seemingly normal in most respects, are much undersized whereas others are much larger than the average. These differences increase with elapsed time and by late spring some of the smallest young are still of a size typical for hatchlings whereas at the other extreme the largest young of the year overlap in size the smallest second year young. Therefore, although the population consists of discrete annual age groups, there is a continuum in size from the smallest to the largest individuals at most times of year. Throughout the first year of life most young are recognizable as members of their cohort. Only a small percentage overlap in size those that are in their second year. Second year snakes are usually recognizable as such, but their size-range has increased and they are overlapped in size by both first- and third-year individuals.

The typical course of early growth is revealed best by comparing mean size of series of young from different times of year with the size of newly hatched individuals to determine the amount of gain in a given time. The course of later growth is revealed best by the records of individuals marked and measured early in life and recaptured after intervals sufficiently long that stunting from the original handling had been overcome and was a relatively minor factor.

At the time of hatching the sexes are already somewhat different in size and proportions; the females are larger with shorter tails. As development proceeds, the differences become more pronounced, with females attaining larger average and maximum sizes. Therefore, data for the sexes need to be separated. In some years hatchlings are not found in substantial numbers until September or even October after the surface soil has been moistened by heavy rain; probably such individuals are already several weeks old and they have had time to grow, utilizing egg yolk still unassimilated at the time of hatching, and then beginning to feed. Thus, the normal

Table 7.—Mean Lengths of Cohorts of Young Males in First and Second Year.

	Year of Origin													
	1957-1967 (composite)		1968		1969		1970		1971		1972		1973	
	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N
First year														
early Sept.					120.4 ± 1.84	14	120.0	14						
late Sept.	124.5	92			122.1 ± 1.08	42	120.5 ± .98	45					122.2 ± 2.37	14
early Oct.			116.8 ± 1.40	16			126.5 ± 1.30	78					125.8 ± 2.18	20
late Oct.			116.2 ± 2.14	15			127.0 ± 2.38	21						
late March									118.4 ± 1.30	38			132.0 ± .69	25
early April	119.5	190	120.5 ± 1.16	95	121.9 ± 1.20	54			121.0 ± 1.95	17				
late April	124.8	165	122.6 ± 1.66	40	122.9 ± .88	90	129.6 ± 3.28	15	122.2 ± 2.82		116.0 ± 1.73	23	131.1 ± 1.41	39
early May	129.0	71			130.0 ± 2.25	31	132.7 ± 1.08	13			122.1 ± 3.82	11	137.1 ± 1.70	27
late May	129.2	25					129.7 ± 5.02	10					136.6 ± 2.41	13
early June	140.5	99			145.9 ± 1.41	23			144.6 ± 1.87				141.8 ± 2.46	18
late June	145.2	67	150.0	11	146.9 ± 2.24	27			145.5 ± 2.10	25			145.5 ± 2.01	24
Second year														
early Sept.	175.2	33					169.5 ± 2.61	15						
late Sept.	180.0	92			172.4 ± 2.34	39			183.8 ± 3.21	20				
early Oct.					172.1 ± 2.75	22								
late Oct.					177.4 ± 4.23	13								
late March	186.0	153	179.2 ± 2.16	37			180.1 ± 1.50	68	188.0 ± 3.02	10				
early April	183.9	130	181.				181.5 ± 1.48	57						
late April	182.5	65	186.9 ± 2.23	28	170.8 ± 3.40	22	186.2 ± 1.53	52	189.0 ± 2.76	12	176.5 ± 4.13	11		
early May	186.5	46			174.6 ± 2.30	21	187.0 ± 2.01	33	185.5 ± .74	33				
late May					178.4 ± 3.00	19	185.5 ± 2.20	22			179.6 ± 5.22	10		
early June			191.7 ± 4.52	13					193.5 ± 2.58	11	179.0 ± 3.70	12		

hatchling size is best determined from young hatched in captivity.

Young were hatched from 21 clutches in 1965, 1967, 1969, 1970 and 1974; 50 males averaged 109.3 ± .91 mm and 33 females averaged 114.1 ± 1.22 mm. Most series of young collected in the field averaged several per cent larger than these laboratory hatched young, and presumably they had made some growth between the time of hatching and the time of capture.

Tables 7 and 8 show mean lengths of young males and young females at biweekly intervals for six different years, and for a composite of 11 earlier years when samples were generally smaller. Each vertical column in the tables traces the growth of one cohort of young snakes from the time of their appearance soon after hatching to an age of about 21 months in late spring. The months of July, August, and November through early March are not included because no samples of snakes were obtained then. Many other biweekly intervals in September, October and March through June of specific years lack data because no snakes were found, or samples were inadequately small. Only samples of ten or more are included.

In some instances average length in a sample is slightly less than for a sample of the same cohort in an earlier period. Such aberrations are due to chance and to the fact that successive samples involved different groups of individuals. In most instances slight gain is indicated for each biweekly interval, but the average increment was small in cool weather just before hibernation and just after emergence. The following figures represent average increments for the several annual samples: late September to early October, 3.63%; early October to late October, 1.32%; late March to early April, 0.48%; early April to late April, 2.08%; late April to early May, 2.16%; early May to late May, 2.72%; late May to early June, 3.29%. Growth is fastest in summer, but few snakes were obtained during late June, July, August and early September. The second-year snakes have increased by an average of 46.7% (males) or 49.8% (females) over the length of first-year young at the time of their emergence from hibernation.

In Tables 7 and 8 some annual cohorts of young are definitely accelerated or retarded compared with others at the same stages in their history. For example, the young hatched in 1973 were larger in April 1974 than the April young of other years. Development may be delayed or hastened by early or late retirement into hibernation, but such early differences tend to become smaller or disappear before the end of the first year.

Another aspect of growth brought out by Tables 7 and 8 is difference between the sexes. In every sample of first-year snakes in which there were 20 or more of each sex, the females averaged larger. In 13 such series, the females were 101.2 per cent to 104.7 per cent of male length, with a combined average of 102.9 per cent. In 11 corresponding series of second-year young, the females were 100.5 to 107.8 per cent of male length, for an average of 104.2 per cent.

Figure 14 is based on the snout-vent lengths of first- and second-year young distributed over the year except for November through early March, and July and August, when too few snakes were found for an adequate sample. It shows that the females are consistently larger than males and that young make rapid growth in their first few weeks. However, growth slows with the advent of cooler weather in autumn. A high proportion of all first-year young are between 120 and 130 mm in length, and the means for both sexes are usually within this range from August through the autumn and spring until May. Those sampled in March and early April are only slightly smaller than those sampled in early May. From late April to early September young make rapid growth, increasing from about 130 mm to about

180 mm; then, during their second autumn, winter and spring gains are relatively slight.

An arbitrary dividing line between second- and third-year snakes is set between 214 and 215 mm in males and between 223 and 224 mm in females, on the basis of the gains made by marked individuals. Some snakes seem to suffer little or no stunting from the effects of processing, and most have overcome the effects within a month. Those recaptured after the lapse of an entire growing season or a longer interval were assumed to have made normal growth, the initial stunting being a relatively minor factor.

Figure 14, showing the growth curve through the tenth year in females and the eleventh year in males, is based upon the records of all marked individuals recaptured after a growing season or a longer interval. Since little growth occurs from September through April, and since nearly all the records are from spring and fall, each record was assigned to a particular age-class, with disregard for fractional years, although the actual age of those classed as two-year-olds, for example, ranged from 24 months to about 33 months. Also, the figure includes data from the series of unmarked young that formed discrete age classes at the time of hatching, and in the fall and spring following hatching. The two-year-old and three-year-old classes are based upon recaptured individuals that were marked as hatchlings. The remaining age-classes are based partly on those marked as hatchlings, but also on those marked as second- and third-year young and recaptured as adults. Because second-year young overlap in size both

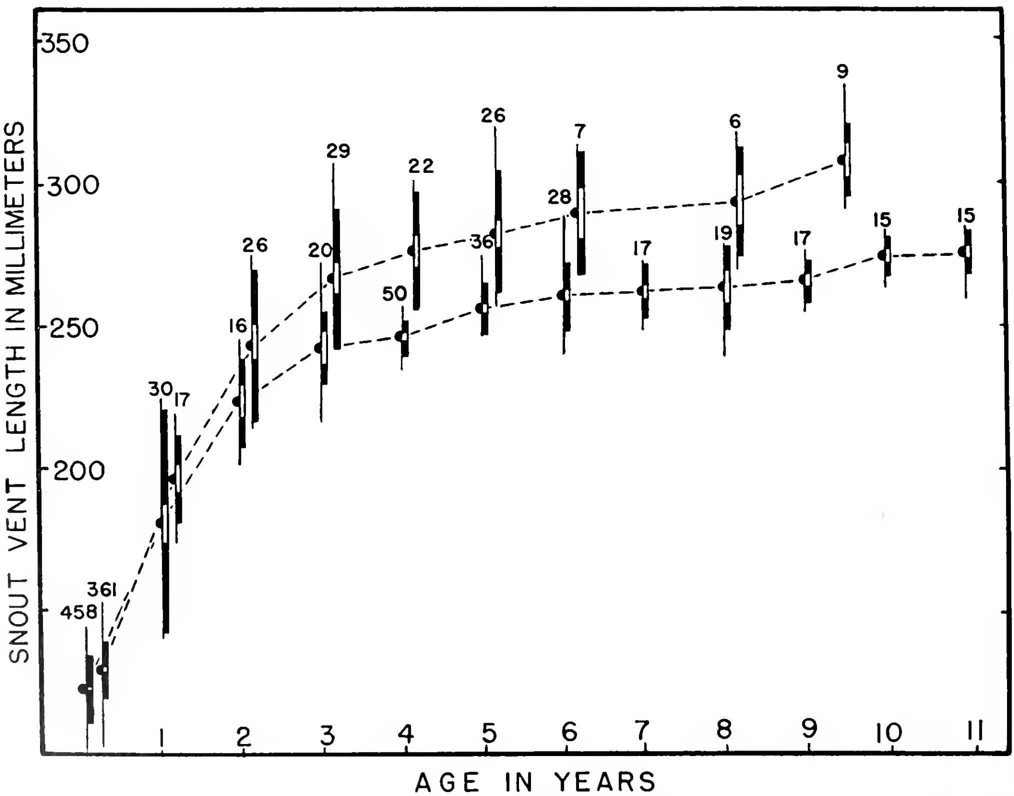

FIG. 14.—Lengths of male and female ringneck snakes marked early in life and recaptured. In each series mean, standard error, standard deviation, range, and sample size are shown. Growth is rapid in the first three years but is slow in the older snakes. Females average larger and plot above males.

TABLE 8.—MEAN LENGTH OF COHORTS OF YOUNG FEMALES IN FIRST AND SECOND YEAR.

	Year of Origin													
	1957-1967 (composite)		1968		1969		1970		1971		1972		1973	
	$\bar{X}$	*N*	$\bar{X}$	*N*	$\bar{X}$	*N*	$\bar{X}$	*N*	$\bar{X}$	*N*	$\bar{X}$	*N*	$\bar{X}$	*N*
First year														
late Sept.	128.0	65			125.0 ± .85	33	126.1 ± 1.02	33					127.8 ± 2.41	17
early Oct.	124.5	100	125.2 ± 2.79	10			130.5 ± 1.31	44	114.9 ± 3.96	11			130.0 ± 1.84	25
late Oct.			122.5 ± 2.29	12	124.0 ± 2.45	10	128.6 ± 2.29							
late March	123.0	53							123.7 ± 1.20	37			133.9 ± 3.47	12
early April	123.8	146	121.7 ± 1.16	63	124.2 ± 1.25	76			122.0 ± 2.86	14				
late April	129.0	133	126.6 ± 2.10	20	128.1 ± .87	67	135.4 ± 2.99	23			123.2 ± 4.18	13	133.0 ± 1.47	33
early May	134.0	68			135.3 ± 1.33	47	132.8 ± 3.39	13			121.9 ± 2.48	20	136.1 ± 2.92	14
late May	135.5	32			140.2 ± 3.57	10	137.7 ± 3.06	12					146.0 ± 3.16	11
early June	144.2	72			148.5 ± .90	15			145.0 ± 2.64	21			148.0 ± 2.28	10
late June	146.8	72	147.0	11	147.5 ± 3.24	17			147.8 ± 3.05	19				
Second year														
early Sept.	181.0	25					179.1 ± 1.08	13						
late Sept.	190.8	55			172.5 ± .98	18								
early Oct.					179.4 ± 2.72	26			194.8 ± 4.27	10				
late Oct.					177.0 ± 5.15	12								
late March							186.0 ± 2.40	47						
early April	192.5	118	193.8 ± 2.94	24			186.0 ± 2.51	72						
late April	193.0	62			182.0 ± 2.71	17	187.5 ± 3.23	25			195.7 ± 6.85	10		
early May	196.6	47	198.0 ± 2.10	30	180.4 ± 2.10	16	194.2 ± 2.77	31						
late May	196.4	34			191.1 ± 4.21	14	188.8 ± 3.20	16						
early June							199.2 ± 2.07	10			180.0 ± 5.41	11		
late June							187.4 ± 3.57	13						

first-year and third-year young, there is some uncertainty as to the age of any individual marked when partly grown and recaptured as an adult. Each such individual was arbitrarily assigned to the age class most typical for snakes of its size at the time of its first capture. The figure shows that growth is most rapid just after hatching and in the growing season following the first hibernation, that in the second full growing season the rate has slowed to about two-thirds and in the third season to one-third, and that thereafter, as adults, the snakes make only slight gains from year to year.

At the time of hatching females are already somewhat longer than males, at an age of 20 months they are five per cent longer, as young adults at 32 months they are nine per cent longer, and in old adults they are 15 per cent longer. Figure 15, showing average and individual length increments in successive years after hatching, indicates that females grow faster. After the third year the snakes gain weight relatively slowly. Actual length gains in millimeters averaged 54, 43, 23, 10, 2 and 4 for the first six years in males, 63, 51, 19, 9, 7 and 3 for females. In the adult snakes the usual annual growth is not much greater than the expected margin of error in

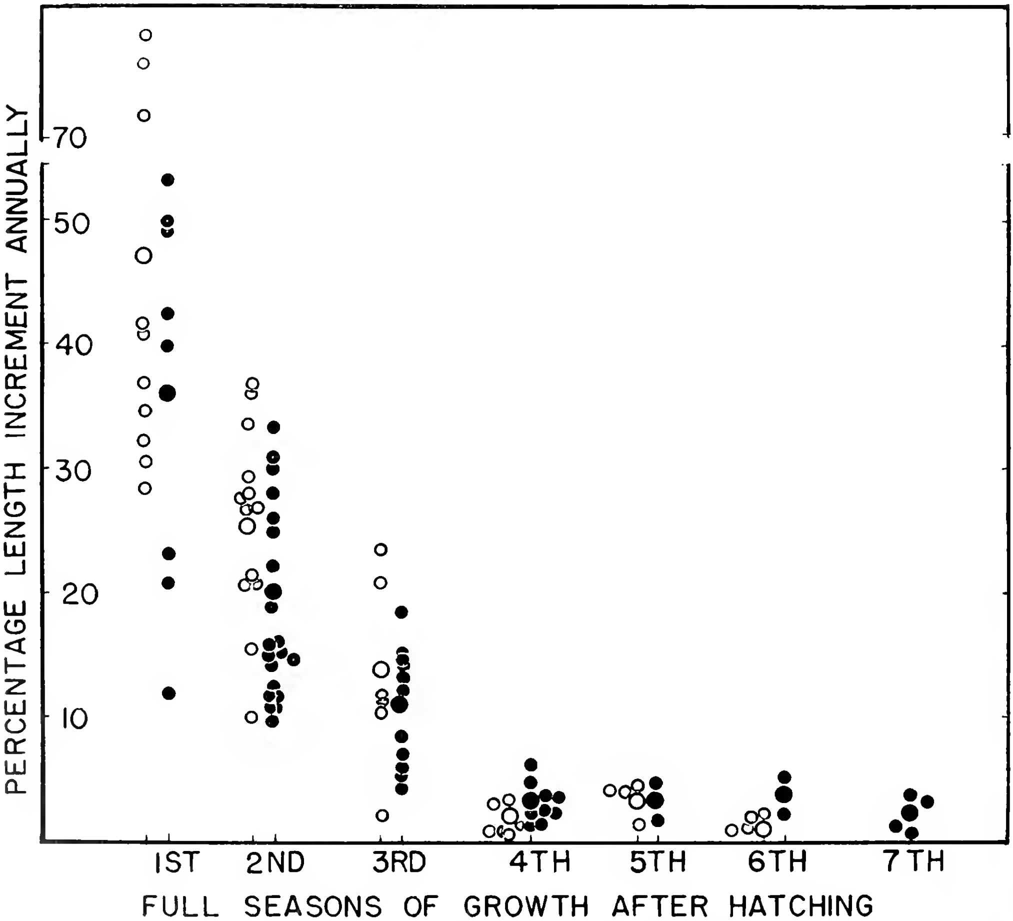

FIG. 15.—Percentage gain in length (S-V) in individual ringneck snakes from one fall and/or spring to the next in successive, or first to seventh, seasons of growth. Open circles, females; solid circles, males; large circles, mean for each series.

measuring; hence, it is difficult to determine. In 42 adult males six years old or more average annual gain was 3.6 ± .41 mm, and in 16 females the corresponding figure was 2.9 ± .89 mm.

Weight.—For snakes of any given length the heaviest individuals generally weighed from 2.5 to 3.0 times as much as the lightest (Fig. 16) and this wide range occurred at all times of years. The heaviest individuals obviously were thriving. Those that were recaptured often had grown much faster than the average rate. The lightest individuals were those that were seriously handicapped by disease, injury or undernourishment. Often such individuals were destined for early elimination.

No well defined seasonal trend in weight was discernible. Snakes emerging from hibernation appeared as well nourished as others, and there was no conspicuous tendency to store quantities of fat at any time of year. However, climatic fluctuations affect amount and availabilty of the snakes' food, and may result in depression or elevation of average weight. Mean weight for the population as a whole may increase more than 40 per cent in response to improved conditions. Sex and size classes are affected similarly. Table 9 compares 10 separate monthly (or bimonthly) samples of 100 snakes each. For each individual the weight is compared with the mean weight for all individuals of that length (Fig. 16). Interest focused on 1966 because snakes recaptured in that year were rather consistently retarded in their growth and precipitation was unusually low. Four of the 10 samples are from 1966; they show that in March of that year, the snakes were 89.5 per cent of normal weight, and that they continued to deteriorate till October when they were only 75.3 per cent of normal weight.

TABLE 9.—DEVIATION FROM MEAN WEIGHT IN MONTHLY SAMPLES, MAINLY FROM PERIODS OF SUBNORMAL PRECIPITATION (FOR EACH OF THE SAMPLES $N = 100$).

Time of Sample	Sample Weight: Percentage of Nomal Weight	Normal Weight: Percentage of Sample Weight
April 1955	106.4	94.0 ± 1.67 (63-128)
October 1959	96.9	103.1 ± .87 (80-130)
Early April 1965	88.8	112.6 ± 1.32 (71-147)
March 1966	89.5	111.7 ± 1.47 (78-171)
June 1966	86.5	115.5 ± 1.08 (82-171)
Aug.-Sept. 1966	88.4	127.7 ± 1.94 (94-183)
October 1966	75.3	132.8 ± 2.34 (87-194)
March 1967	84.7	118.0 ± 1.73 (86-163)
September 1970	104.5	95.6 ± 1.88 (67-155)
March-April 1971	93.0	107.4 ± 1.95 (65-180)

POPULATION DENSITY

The secretive habits of snakes in general render them difficult subjects for census. Few figures concerning population density have been published, and in general these inspire little confidence. The most satisfactory censuses of natural populations are those in which every individual on a sample area of representative habitat can be seen and counted in the course of a brief sampling period. Since ringneck snakes are rarely found away from shelter, best information about their numbers can be obtained by moving the sorts of objects they use for shelter. Where such objects are abundant in favorable habitat, it is evident that the snakes attain high population densities, as many may be found within a small area. However, it is doubtful whether all those present, or even a high percentage of them, can be found at any one time.

Most revealing data concerning actual abundance were obtained on 13 April 1968; in approximately half an hour of field work 279 ringneck snakes were captured in Quarry Field, a nearly flat, triangular hilltop area of 3.8 hectares bounded on two sides by steep rocky slopes, and on the third by a county road. All snakes were found in aggregations beneath approximately two dozen corrugated metal strips that were scattered about the field.

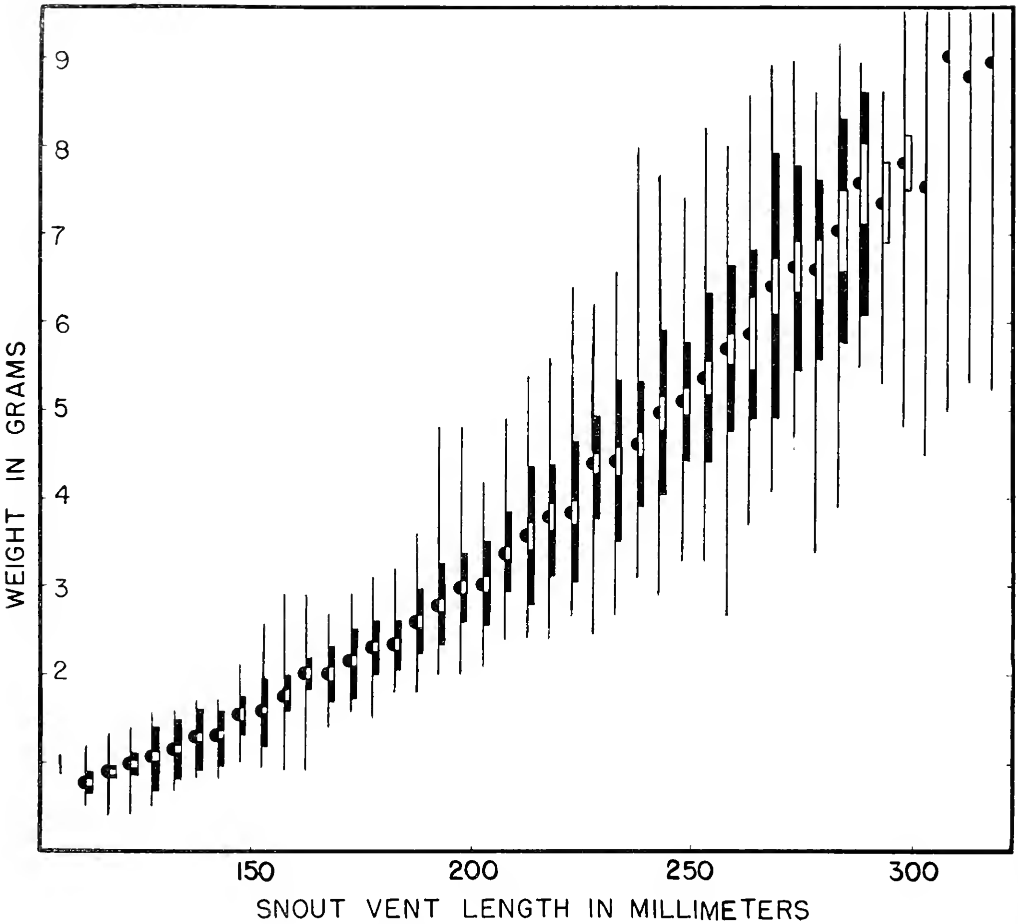

FIG. 16.—Relationship of length to weight in ringneck snakes, grouped in five-millimeter intervals. For each length interval sample the standard error, and standard deviation and range of weight are shown.

The 279 snakes caught on this occasion represent a minimum population of 73.5 per hectare. On numerous other occasions from 1964 through 1974, the same series of shelters (and others added subsequently) were turned in routine search but on no other occasion were so many snakes found at one time. In evaluating the significance of the series of snakes to determination of population density, it is necessary to know whether individuals were residents or transients, how large an area might be covered by individuals and to what extent the local population was using the specific shelters checked. This same 3.8-hectare field was the locale of intensive population study for four years before the collection and seven years afterward (including the 1968 season); therefore, much information is available about some of the individual snakes caught. Of the 279 total, 156 were caught only once, on 13 April 1968, never before or after. Fifty-three others were caught one or more times before that date but not afterward; 51 were recaptured subsequently but not before, and 19 were caught both before and afterward. The snakes in this group that were caught on other occasions were distributed by years as follows: 4 in 1964, 7 in 1965, 32 in 1966, 24 in 1967, 21 in 1968 (7 before 13 April and 14 after that date), 27 in 1969, 20 in 1970, 4 in 1971, 5 in 1972, 5 in 1973 and 4 in 1974. The 279 snakes included 245 adults (203 males and 42 females), 24 second-year young (17 males and 7 females), and 10 first-year young (6 males and 4 females). The sample has a high proportion of adult males (believed to be especially active in sexual search at this time and place); immatures constitute only 12.2 per cent.

The 13 April search that yielded 279 snakes resulted in the escape of many others because the aggregations under the metal strips scattered in all directions when they were uncovered. Females and young, missing from this sample that consisted mostly of adult males, may have been present within the field but less inclined to trail other individuals and form aggregations (see section on Composition of the Population). Or they may have been absent from the field, still concentrated at hilltop limestone outcrops where they had hibernated.

Consideration of all available data suggests that the 279 snakes captured on 13 April 1968 were mostly residents of Quarry Field and that they were only a small part of the population present there. Subsequent study by Richard L. Lattis, trailing ringneck snakes equipped with radioactive tags, has shown that the metal strips are not focal points of the snakes' activities, and are not used regularly by any individuals nor do they constitute an essential part of the local habitat. Instead the strips are used from time to time by snakes in the immediate vicinity when they happen to provide shelter with optimal thermal and hygric conditions. Most of the snakes most of the time are using shelters such as the surface mat of dead vegetation, where they cannot be found readily. Although many of the 279 snakes in this sample were caught at other times, over a ten-year period, they collectively never made up more than a small percentage of any one sample.

In the spring of 1968 after 13 April, there was little opportunity for further field work, but 23 snakes were captured on 21 April and eight on 10 May and these 31 included only one recapture from the 279 on 13 April. This one-to-31 ratio suggests that the original sample of 279 represented an actual population of 8650. This figure, based on just one recapture, is obviously of little significance but it does serve to demonstrate that the 279 snakes of the 13 April sample were drawn from a much larger pool and their marking did not constitute substantial progress in attaining a fully-marked population on the study area of Quarry Field. In late September and October of 1968, collections of snakes were made in Quarry Field on 16 days and a combined sample of 184 was obtained, not including the hatchlings that had emerged in late summer. This sample included 14 individuals from the 13 April collection. The one-to-13 ratio in this collection suggests a total population in spring of 13 X 279 or 3630 (950 per hectare) in this field. However, the long interval between 13 April and the October-November resampling lessens the value of the calculation. Population changes, with dispersal and replacement of some individuals, would have occurred in the interval.

A population index based upon capture-mark-recapture is useful only if certain assumptions can be made about the stability and spatial relationships of the population: it should be limited to a definite area and the individuals marked should distribute themselves randomly; their survivorship or difficulty of capture should not be affected; there should be no reproduction in the population or else it should be measurable. From what is known about the *Diadophis* population, the following statements bearing upon these problems may be made. 1. Most individuals most of the time stay within areas much smaller than those sampled. There is sometimes a shift between summer range and hibernaculum or place of egg-laying. 2. As in other vertebrates some individuals may wander in a random manner as transients, but most stay in the same place, and sometimes are recaptured within a few meters of a former capture site after several years. 3. Individuals experience some deleterious effects from marking and handling, but certainly most survive. No definite instances of mortality were observed. 4. Reproduction occurs only once in the annual cycle and young constitute a discrete size group distinguishable from older snakes, so that they do not complicate capture-recapture ratios.

In view of these traits and in view of the fact that no other method is available to measure populations even in general terms, it seems worthwhile to apply a "Petersen Index" to the *Diadophis* population studied. Some workers have rejected capture-recapture indices as a means of censusing snakes on the grounds that the published figures from studies of this type are too erratic to be acceptable. Yet there is nothing in the known population ecology of snakes that makes capture-mark-recapture technique inapplicable to them. In general, snakes are difficult to census because they are secretive and it is difficult to obtain adequate samples. However, each case should be judged on its own merits, depending on the size of the sample and the extent to which the theoretical assumptions of a Petersen Index can be demonstrated to be satisfied.

In my study Quarry Field (3.80 hectares) and House Field (5.76 hectares) were sampled on hundreds of occasions but with the possible exception of 13 April 1968 the snakes captured on any one day were too few to be used as a separate sample. By combining many day to day samples, adequate presampling and resampling periods within a spring or fall season were obtained in several instances.

Table 10 shows seven censuses in five different years in House Field and

TABLE 10.—POPULATION DENSITIES OF RINGNECK SNAKES ON TWO STUDY AREAS, CALCULATED FROM MARK-CAPTURE-RECAPTURE SAMPLES.

Area and Year	Presampling Period	Resampling Period	Number in Presampling Period	Ratio of Recaptures to Total in Resampling Period	Estimated Population	Estimated Density; Snakes Per Hectare
Quarry Field						
1966	March, April 1-15	April 16-30, May	253	10 to 278	7002	1849
1967	March, April 1-15	April 16-30, May	182	6 to 90	2730	719
1969	March-April	May-June	346	12 to 187	5400	1421
1970	March-April	May-June	57	6 to 442	4200	1105
House Field						
1965	July-August-September	October-November	386	23 to 267	4485	774
1966	March, April 1-15	April 16-30, May	332	17 to 532	10400	1808
1967	March, April 1-15	April 16-30, May-June	238	8 to 230	6840	1188

Quarry Field. Calculated figures for population density ranged from 719 to 1849 per hectare, with a mean of 1266 per hectare for all seven calculations combined. Individuals are long-lived, and year-to-year variation in reproductive success would not be sufficient to bring about the fluctuations which must be caused by biased or inadequately small samples. The highest and lowest figures are probably far from the mark.

Rapid seasonal changes in kind and amount of activity and in the ratios of sex- and age-groups in samples hinders census and prevents effective use of refinements of the capture-recapture index, such as have been proposed in the "Hayne Method" and the "Jolly Method." A crude capture-recapture index does not provide a precise measure of the population, as has been demonstrated by several investigators. Nevertheless, in this instance, and with secretive animals in general, it does provide better information about numbers than do direct counts, and at least indicates the order of magnitude of the population. It suggests that in favorable habitat population densities of ringneck snakes are often between 1000 and 1500 per hectare.

It cannot be stated with any degree of assurance whether the census figures obtained tend to err on the low side or the high side. Even the lowest census figure, of 719 snakes per hectare, would seem excessively high for most kinds of vertebrates, but all evidence suggests that *Diadophis punctatus* actually does attain high densities. The methods of obtaining samples, by returning regularly to certain favored spots to turn sheltering objects or to check live-traps, would tend to favor recapture of certain localized individuals and would increase the ratio of recaptures to new captures, resulting in an erroneously low census figure. On the other hand, wandering tendencies of some individuals, which might leave the study area after being marked, with replacement by newcomers, would result in an erroneously low recapture ratio and calculation of a figure for the population that is too high.

COMPOSITION OF THE POPULATION

Age structure.—Age structure of the adult population was calculated after analysis of the records of individuals marked while young and recaptured as adults (Figs. 14-19, Tables 11-14). These records, combined, show that length is highly correlated with age, so that each individual may be assigned to a most probable age group on the basis of its measurements. Within each age group lengths vary over a wide range but tend to form normal curves, with a clustering of records near the mean and progressively fewer in successive stages of deviation from the mean. Each age group exceeds younger age groups in mean length, but successive annual increments become progressively smaller. Samples are smallest for the relatively old snakes, so that the trends of growth and survival become increasingly obscure.

The graph in Figure 14 shows some inconsistencies in the older age groups; for instance ten-year-old males in the sample averaged slightly larger (274.5 ± 1.84 mm S-V) than eleven-year-olds (273.0 ± 2.10). Such irregularities may result from inclusion of occasional stunted individuals or those of unusually accelerated growth. Recognizing that growth continues in adults, but becomes progressively slower with increasing age, and that there is a consistent difference in sizes of the sexes at any given age, the growth curve has been adjusted by slight alterations as shown in Table 14. The table indicates that the annual reduction from any age class to the next older class is consistently between 20 and 30 per cent, and averages 23.4 per cent for males and 26.8 per cent for females. For example, the 1458 first-year males make up 25.2 per cent of the entire sample of 5814 males and the 92 males in the size range (275-277 mm) typical of eleventh year individuals make

TABLE 11.—COMPOSITION OF A POPULATION OF 9162 *Diadophis punctatus* CAPTURED AND MARKED ON THE RESERVATION, 1958-1969.

	Number of Males	Size Range of Males	Number of Females	Size Range of Females	Total Number	Male to Female Ratio
Adults	3436	215-351	1851	221-392	5416	1.85 to 1
Second-year young	920	147-214	513	160-220	1444	1.79 to 1
First-year young	1458	90-146	984	85-159	2552	1.48 to 1
Total	5814	90-351	3348	85-392	9162	1.73 to 1

up 23.7 per cent of the snakes that are of this size or larger (presumably more than 10 years old). Non-age-specific annual mortality of approximately one-fourth for both males and females is implied by the figures. Incidentally the figures show a gradual increase in the sexual difference in size, with females averaging 109 per cent of male length in newly matured third-year snakes, but increasing to 112.0 per cent in the eighth-year group and 115.0 per cent in the 14th year group.

Although any individual can be assigned to a "most probable" age on the basis of size alone, there is no certainty that such allocations are correct. The chances that such assignments will err by a year or more are increased greatly in the old snakes, in which any one age class includes individuals that cover a wide range of size.

Behavior differs between the sexes and between young and adults so that most field samples are probably subject to some bias, with certain classes better represented than others. Table 11 divides the population into six classes: adult males (third year and older), adult females (third year and older), first-year males and females, and second-year males and females. The table includes the 9162 snakes caught over a 12-year-period, when those captured were individually marked and released. Recaptures are not included. These snakes were not all contemporaneous; rather, the 12-year interval spanned many generations, with constantly changing ratios of the sexes and of age groups. However, all are here combined to represent

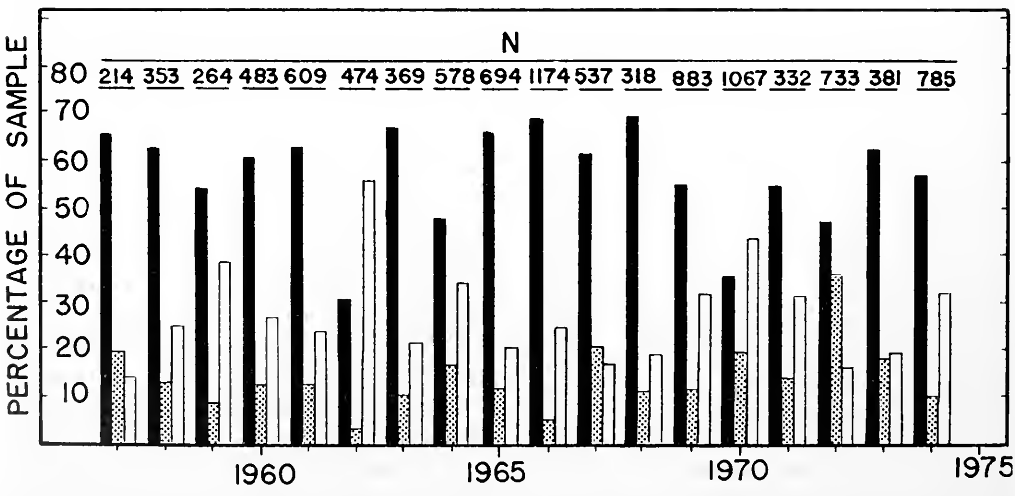

FIG. 17.—Percentages of adults (solid columns), second-year young (shaded columns), and first-year young (open columns) in annual spring population samples from The University of Kansas Natural History Reservation and nearby areas over an 18-year period.

one population in this composite, minimizing the seasonal and year-to-year differences that characterize the smaller samples. In general the samples represent either fall or spring in the pause between the summer growth periods; therefore, there are discrete annual age groups and in the younger snakes there are fairly distinct size groups.

The 3436 adult males make up 39 per cent of the total in Table 11 and are much better represented than any of the other five classes. For example, the adult male to adult female ratio is 1.85 to 1. However, Table 12 shows that this ratio changes throughout the season of activity, with females constituting only 23.6 per cent (1 to 4.24 males) in the early September sample of adults but increasing to 71.0 per cent of the early July sample. Throughout the spring months, when the snakes are found in greatest numbers, females comprise less than 40 per cent of adult samples, and often less than 30 per cent. In the hot weather of June and July, the snakes are much harder to find. Samples are small then but the ratio of females rises. These females are gravid and their relative conspicuousness seems to be correlated with a tendency to frequent superficial situations where body temperatures are readily elevated by basking. The remainder of the population retreats to deeper shelters. In late summer after egg laying and in early fall females again become relatively scarce in samples.

TABLE 12.—CHANGING SEX RATIO OF ADULT *Diadophis punctatus* THROUGHOUT SEASON OF ACTIVITY.

Time period	Total Sample	Number of males	Number of females
16-31 March	285	182(63.9%)	103(36.1%)
1-15 April	1291	927(71.9%)	364(28.1%)
16-30 April	1187	818(68.9%)	369(31.1%)
1-15 May	939	662(70.5%)	277(29.5%)
16-31 May	509	323(63.4%)	186(36.6%)
1-15 June	351	191(45.5%)	160(54.5%)
16-30 June	297	90(30.5%)	207(69.5%)
1-15 July	83	24(29.0%)	59(71.0%)
16-31 July	50	26(52.0%)	24(48.0%)
1-15 August	57	23(40.4%)	34(59.6%)
16-31 August	79	50(63.3%)	29(36.7%)
1-15 September	288	220(76.4%)	68(23.6%)
16-30 September	667	500(74.8%)	167(25.2%)
1-15 October	560	385(68.7%)	175(31.3%)
16-31 October	268	141(52.6%)	127(47.4%)
1-15 November	18	11(61.2%)	7(38.8%)

Sex-ratio.—The seasonally fluctuating sex ratio in samples raises the question whether males are actually more numerous than females, or are merely easier to find. The following ratios of adult female to adult male captures indicate that females, regardless of their actual numbers, are more secretive and less readily taken:

Individuals with only one capture: 1 female to 1.85 males
Individuals with 2 or 3 captures: 1 female to 3.34 males
Individuals with 4 to 12 captures: 1 female to 6.85 males

There may be some bias in most samples arising from the fact that sexually mature males are more active than mature females, or immatures of either sex, causing these males to be found more often.

Physiological and behavorial differences between the sexes must result in some differential mortality. Female mortality may be a little higher, judging from the fact that the oldest individuals recorded were all males (Table 13). However, the figures in Table 14 suggest that mortality rates are not much different in the sexes. Presumably in preadolescent young the sexes are alike in behavior or at least differ much less than adults, hence more acceptable ratios can be obtained from them. As shown in Table 11, males are more numerous than females even in the first-year young with an approximate ratio of 1.48 to 1. First-year and second-year young combined made up 40.8 per cent and 43.0 per cent,

TABLE 13.—RECORDS OF LARGE (AND OLD) MALES OF *Diadophis punctatus* CAPTURED AND RECAPTURED, INDICATING POTENTIAL LONGEVITY.

Dates of Capture And Recapture	Size (S-V) at Capture And Recapture	Time Span of Records (Years)	Most Probable Age First Capture	Most Probable Age Last Capture	Possible Age Range at Latest Record
25 April 1966 - 11 Sept. 1973	260-284	8	7	15	10-17+
5 May 1966 - 20 April 1970	274-282	4	10	14	9-14+
18 April 1966 - 10 May 1968	276-293	2	11	13	8-15+
12 May 1966 - 16 May 1970	283-291	4	13 or more	17 or more	13-19+
9 May 1966 - 13 April 1970	273-280	4	10	14	9-14+
2 Oct. 1964 - 2 Oct. 1970[a]	264-290	6	8	14	9-14+
25 April 1966 - 9 April 1970[b]	267-278	4	8	12	6-12+
17 April 1965 - 30 May 1970[c]	267-268	5	8	13	-14+
4 Sept. 1965 - 13 Oct. 1968	272-275	3	10	13	7-13+
8 April 1965 - 15 April 1970	265-263	5	8	13	8-13+
4 April 1966 - 17 April 1974	267-281	8	8	16	7-16+
13 April 1968 - 17 April 1974	273-283	6	10	16	9-16+
13 April 1968 - 14 May 1974	274-282	6	10	16	9-16+

[a] Recaptured also in April 1967, 1968, 1969 and 1970.
[b] Recaptured also in April 1970.
[c] Recaptured also in May 1968.

respectively, of the male and female samples in Table 11.

Figures 17 and 18 show the changing ratios of adults to first-year young and to second-year young over an 18-year period. The ratios are believed to reflect varying reproductive success in different years. Also, they are affected by the times and places that samples were collected. In some years large concentrations of young were found in nursery areas, whereas in other years the collections were made mostly in the areas where adults predominated.

Fecund females are estimated to comprise approximately 20.2 per cent of the population. If the 1851 females represented in Figure 19 produced an aver-

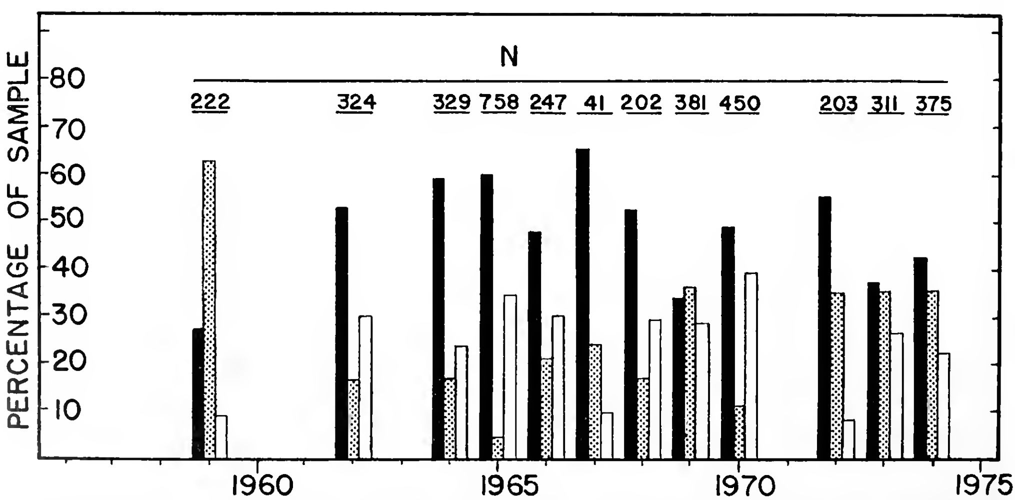

FIG. 18.—Percentages of adults (solid columns), second-year young (shaded colmuns), and first-year young (open columns) in annual fall population samples from the University of Kansas Natural History Reservation and nearby areas, 1959 to 1974.

age of 3.89 eggs per clutch, their total output would amount to 7210 eggs and this annual increment would add 78.6 per cent to the spring population. It is calculated that by the following spring the hatchlings from these 7210 eggs would be reduced by approximately two-thirds to 2442 (1458 males, 984 females). The 66 per cent mortality would be attributable to several causes, including resorption or abortion of eggs, infertility or inviability of some of those laid, genetically defective hatchlings, predation on hatchlings and winterkill of the hibernating young.

The age pyramid in Figure 19 is based upon the actual numbers of snakes captured, but shows also the numbers of missing adult and second-year females that might have been present but undetected (shaded ends of columns) if the sex ratio of 1.48 males to 1 female that was found in hatchlings is the real ratio for the older snakes also.

PREDATION

There are few published records of predation on *Diadophis*. In the present study 94 records of eight species of predators on the Reservation and nearby areas were assembled; large series of pellets of raptors and scats of snakes were examined, hawk nests were visited on many occasions to check for remains of prey, and hundreds of live snakes of other kinds were palped to identify food objects. The records of predation on *Diadophis* included 35 by *Agkistrodon contortrix*, 25 by *Buteo jamaicensis*, 15 by *Coluber constrictor*, 13 by *Buteo platypterus*, 2 by *Lampropeltis triangulum* and 1 each by *Bubo virginianus*, *Crotalus horridus* and *Rana catesbeiana* (Table 15). Sample size varied from 2763 stomach examinations of *Rana catesbeiana* to only 20 records of feeding in *Lampropeltis triangulum*. The 192 pellets of *Bubo virginianus* represent mainly the colder half of the year, with reptiles including *Diadophis* probably much less well represented than they would have been in summer. Table 15 shows sample sizes and frequency of *Diadophis* in food for the eight predator species, and attempts to show the relative severity of predation on the basis of

TABLE 14.—SAMPLE OF 9162 RINGNECK SNAKES CAPTURED OVER A 12-YEAR PERIOD (1958-1969) ARRANGED IN SIZE GROUPS AND SUPPOSED ANNUAL AGE GROUPS TO SHOW PROGRESSIVE REDUCTION IN NUMBERS WITH INCREASING AGE.

	MALES				FEMALES			
Most Probable Age in Years	Most typical Size Range (mm S-V)	Actual Number In Size Class	Total Alive At Start of Year	Percent Lost During Year	Most Typical Size Range (mm S-V)	Actual Number In Size Class	Total Alive At Start of Year	Percent Lost During Year
1st	110-146	1458	5814	25.2	110-159	984	3348	29.4
2nd	147-214	920	4356	21.1	160-223	513	2364	21.6
3rd	215-233	851	3436	24.7	224-256	464	1854	25.1
4th	234-245	673	2585	26.0	257-272	380	1387	27.4
5th	246-253	484	1912	25.3	273-280	231	1007	21.6
6th	254-258	300	1428	21.0	281-287	169	776	21.8
7th	259-263	261	1128	23.2	288-294	163	607	26.8
8th	264-267	211	867	23.4	295-300	101	444	22.8
9th	268-271	154	656	23.4	301-305	89	343	26.0
10th	272-274	114	502	22.7	306-310	74	254	29.1
11th	275-277	92	388	23.7	311-315	49	180	27.2
12th	278-280	76	296	26.7	316-320	33	131	25.2
13th	281-283	56	220	25.4	321-325	27	98	27.5
14th	284-286	43	164	26.2	326-330	21	71	29.6
15th or older	287-351	--------	121	------	331-392	------	50	------

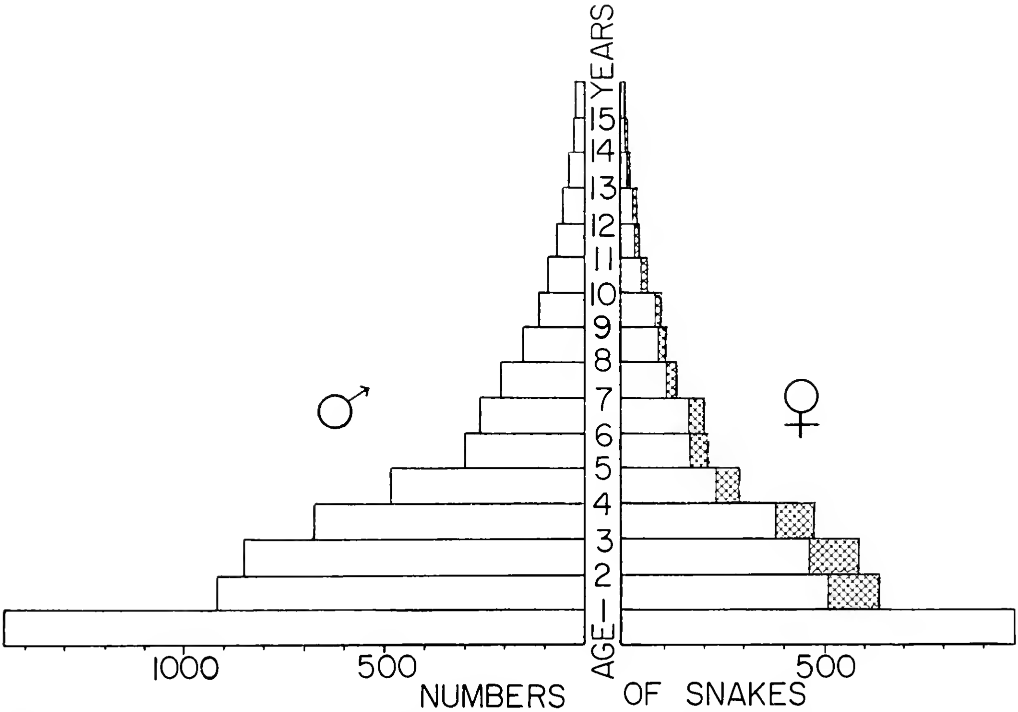

FIG. 19.—Age pyramid showing relative numbers of successive annual age classes of male and female *Diadophis punctatus*, based on figures in Table 14. Shaded portions of columns on female side represent a part of the population not actually recorded but suspected to be present if the ratio of 1.42 males to 1 female found in first-year young is correct for adults also.

frequency of *Diadophis* in the food, population density of the predator, and frequency of its feeding. Number of meals consumed annually by each kind of predator on the 590-acre Reservation have been estimated from censuses of the predators and observations on the frequencies of their feeding. Most kinds are present and active only in the warmer part of the year. For *Bubo virginianus* and *Buteo jamaicensis*, both present throughout the entire year, the estimated total number of meals is divided by two because it is unlikely that predation on *Diadophis* would occur during the colder half of the year.

The figures suggest that the copperhead and blue racer combined account for 94 per cent of the known predation whereas none of the other six predators accounts for as much as 1.5 per cent. The combined kill of the eight known predators would account for approximately 1700 *Diadophis* annually, a little less than 7.4 per hectare on the Reservation. However, this toll seems trivial in view of the finding that *Diadophis* attains population densities of several hundred per hectare over extensive areas of favorable habitat. Presumably the population is regulated by some other mortality factors.

Other predators may be even more important than those studied, although no records of their predation on *Diadophis* were obtained. The eastern mole *Scalopus aquaticus* is one such suspect. It is known to feed largely on earthworms and other invertebrates, but feeding experiments with captive moles on the Reservation demonstrated that they would catch and eat small reptiles at every opportunity. The spotted skunk *(Spilogale putorius)*, striped skunk *(Mephitis mephitis)* and opossum *(Didelphis marsupialis)* all are known to

TABLE 15.—PREDATION ON *Diadophis punctatus* AT THE UNIVERSITY OF KANSAS NATURAL HISTORY RESERVATION

	Kind of Predator							
	Bubo virginianus	*Buteo jamaicensis*	*Buteo platypterus*	*Agkistrodon contortrix*	*Coluber constrictor*	*Lampropeltis triangulum*	*Crotalus horridus*	*Rana catesbeiana*[a]
Size of sample	192 pellets	1322 prey items	138 prey items	512 prey items	1008 prey items	20 prey items	23 prey items	2763 stomachs (971 with food)
Number of *Diadophis*	1	25	13	35	15	2	1	1
Percentage frequency of *Diadophis*	.005	.019	.094	.068	.014	.100	.043	.001
Estimated Population of Predator	10	4	2	2180	1200	10	10	1000
Estimated Number of Meals Taken Annually	3650	1460	360	17440	30000	250	100	2500
Number of *Diadophis* Eaten Annually	9.5	13.8	17	1191	417	25	4.3	25
Percentage of *Diadophis* in Combined Sample	.56	.81	1.00	70.00	24.42	1.47	.25	1.47

[a] Smith, 1973

feed upon small reptiles, and, as all are fairly common on the Reservation, they may be among the major predators on *Diadophis* there.

The wood mouse *Peromyscus leucopus* is known to take a variety of animal matter in its food. Evidence that it may prey on hibernating *Diadophis* was obtained in November and December of 1964, after several of these and other snakes were released at known hibernacula at hilltop limestone outcrops, with thermisters implanted and with fine and extremely pliable wires attached to them and extending to the surface. After several weeks it was found that all the wires had been cut by the mice and there was evidence that the reptiles themselves had been eaten. Perhaps in these instances the snakes were handicapped by the attached wires, so that they were prevented from reaching the deep and secure shelters where they would have hibernated. However any small reptile hibernating where its body surface is accessible to mice would seem to be vulnerable to predation. The shrew *Blarina brevicauda* also is a potential predator, especially on hatchlings. Many of the snakes bore scars on their bodies, and especially on their tails, that could have been interpreted as shrew bites.

These worm-sized snakes, especially the smaller individuals are potential prey for birds other than raptors, such as the crow *Corvus brachyrhynchos,* Blue Jay *Cyanocitta cristata,* Grackle *Quiscalus quiscula,* Yellow-billed Cuckoo *Coccyzus americanus* and Brown Thrasher *Toxostoma rufum.*

Disease may be an important mortality factor. One common ailment caused the snakes to develop blisterlike swellings in the skin, and sometimes these produced open lesions. The snakes so afflicted were in varying degrees emaciated and sickly in appearance. Ringneck snakes kept in confinement dehydrated rapidly unless they had access to water, but those kept in damp surroundings rapidly developed the ailment described, and succumbed. Blanchard, Gilreath and Blanchard (in press) described this same ailment in the population that they studied in northern Michigan, and Henderson (1970) was handicapped by it in his study of food and water consumption in confined ringneck snakes.

Winterkill may involve considerable mortality in addition to predation of the hibernating snakes. Since *Diadophis* lacks capacity for digging and can only follow existing passageways or force its way through loose soil, entombment or entrapment might frequently occur through deposition or compaction of the soil around the hibernating snake. Freezing is also a potential source of winter mortality, but the species penetrates into regions having much more severe winter climates than that of northeastern Kansas, where this must be a relatively minor factor.

DISCUSSION

Compared with small vertebrates in general, the ringneck snake is *K*-selected (*sensu* Dobzhansky, 1951; MacArthur and Wilson, 1967; Pianka, 1970) in the following respects: sexual maturity delayed (first breeding in third year), brood size reduced (3.9 eggs per clutch, produced once annually), young relatively large and well developed at hatching (36% of maternal length and 12% of maternal weight), life expectancy increased (annual mortality in adults less than 25 per cent, with some individuals attaining ages of 15 years or more). All these traits make for stability of populations and except for the climax vegetation itself the ringneck is one of the most stable elements in its community. Snakes in general are notable for longevity, and associated stability of populations. However, considering the small size of the ringneck, it has progressed farther than most in the direction of *K*-selection, a trend correlated with its secretive and partly subterranean habits.

The ringneck snake is a predator on various sorts of small vertebrates and invertebrates but the trend of food habits differs in different parts of the range. The locale of this field study is in the ecotone between deciduous forest and grassland, at the eastern edge of the Great Plains, near the center of the geographic range of the ringneck snake, which is a wide-ranging, polytypic species. Selective pressures in this ecotonal region have produced a population different from any in other parts of the range, but many of the differences are subtle. Snakes of the population studied are relatively small and stubby, highly variable in extent and pattern of dark ventral markings, and more secretive and subterranean in habits as compared with eastern populations (but perhaps less so than far western and southwestern populations). In feeding they have become specialists dependent almost entirely on earthworms, whereas elsewhere populations are much more versatile but with a tendency to specialize on plethodont salamanders (northeastern United States and Appalachian region), on insects and other invertebrates (southeastern United States) or on small reptiles (Southwest).

Geographic variation in size and morphological characters occurs along with variation in food habits, but the morphological variation does not closely parallel the behavioral variation. Gehlbach (1974) noted that in *Diadophis punctatus arnyi* of Texas, near the range of *D. p. regalis,* size remains relatively small, but *arnyi* in that area resembles *regalis* in its ophiphagous habits. When individuals of the two subspecies were confined together, mating occurred despite the disparity in size. Cannibalism did not occur in these mixed pairs although other small snakes were readily eaten when confined with the large *D. p. regalis.* Gehlbach found intergradation between the subspecies *arnyi* and *regalis* in central and western Texas, but in the Guadalupe Mountains he found isolated populations of both types with no interbreeding. Gehlbach speculated that small ringneck snakes similar to *arnyi* and the more eastern subspecies, of worm-eating habits and mesic habitats, are ancestral and that the large, ophiphagous *regalis*-type populations evolved from these snakes in Pliocene Madro-Tertiary woodlands. An alternative possibility is that *regalis* is the more primitive and that *arnyi* and far eastern and far western subspecies are derived from a *regalis*-like ancestor. Although evolution conceivably could have proceeded in either direction, *regalis* seems more generalized, that is, more like related genera of xenodontine snakes, but with less typical exhibition of the characters that distinguish *Diadophis*. Among such generalized characters are: euryphagous habits and predation on small vertebrates, lack of a neck ring, and large body size associated with large numbers of ventral and subcaudal scales and with 17 body scale rows, whereas other subspecies have only 15 to 13 rows.

The abundance and availability of earthworms as a food supply has permitted attainment of remarkably high population density and biomass by the snakes in the area of my study. Throughout much of its range the ringneck is one of the less common species of snakes, but in northeastern Kansas it probably outnumbers all other species combined. On the basis of known population structure and the average weight of individuals of different sizes it is calculated that 3.6 grams is a typical weight. A population of 1266 snakes per hectare (the average of seven capture-recapture censuses) would thus have a biomass of 4.58 kilograms. Of local vertebrates only the prairie vole *(Microtus ochrogaster)* has been found to attain higher biomass over extensive areas, with 7.41 kg per hectare in an actual sample, but the vole is a primary consumer, and its population is subject to rapid and drastic change. Other vertebrates of the Reservation known to occur, at times, in biomass exceeding 1 kg per hectare include the cottontail, *Sylvilagus floridanus*, 3.88 kg (in the only instance in which a population was adequately measured; however, it probably often exceeds this figure and is the most important primary consumer among the local vertebrates); slender glass lizard, *Ophisaurus attenuatus*, 1.96 kg (in brushy former pastures dominated by tall brome grass); Great Plains skink, *Eumeces obsoletus*, 1.86 kg (in rocky, open hilltop habitat in 1949, but subsequently almost eliminated by unfavorable changes in the course of vegetational succession); worm snake, *Carphophis vermis*, 1.67 kg (on rocky, wooded hillside and hilltop); five-lined skink, *Eumeces fasciatus*, 1.34 kg (in open woodland soon after livestock were removed, but successional trends subsequently caused marked reduction); copperhead *Agkistrodon contortrix*, 1.23 kg; cotton rat, *Sigmodon hispidus*, 1.11 kg (probably often exceeded by this primary consumer, but the cotton rat is also subject to drastic reduction and is usually much below this figure even at times and places where habitat is favorable).

These incomplete and preliminary figures indicate that *Diadophis* attains biomass levels comparable with those of the most abundant vertebrate primary consumers and much exceeding the other local reptiles that feed upon invertebrates such as insects and annelids.

Traits peculiar to the local population of *Diadophis* must have arisen over a long period of selection and adjustment to climate, habitat and biotic associates. On the other hand profound changes in the species' ecology must have been brought about within the past 125 years as the region was altered from its original state by settlement, agriculture and industry. Within the ecotone between deciduous forest and prairie, there was formerly an abrupt transition from woodland to grassland, but tree-cutting, elimination of prairie fires, and pasturing of livestock destroyed the clear-cut boundaries and created a much more extensive transitional zone with a mixture of woodland and prairie types of vegetation that provided better habitat for ringneck snakes than either type in its pure form. Meanwhile the common and adaptable earthworm *Allolobophora caliginosa*, introduced from the Old World, became established in a thriving population that provided an abundant new food supply for the ringneck snake. Although there are on record no actual observations of population changes in *Diadophis*, it may be speculated that the vastly improved habitat and food supply resulting from man's alteration of the original forest-prairie ecotone, caused a population explosion of the snakes. Perhaps they are more abundant now than ever before.

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