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NATURAL HISTORY OF A RELICTUAL POPULATION
OF THE PRAIRIE VOLE, *MICROTUS OCHROGASTER*,
IN SOUTHWESTERN OKLAHOMA

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The prairie vole, *Microtus ochrogaster* (Wagner, 1842), is indigenous to central North American prairies. A population of these voles was discovered in the early 1970s on the east range of the United States Army's military installation at Fort Sill, Oklahoma, extending the southern limit of the known range as previously mapped by Hall (1981) and Jones *et al.* (1985). George Johnson, Post Agronomist (personal communication), first observed vole skulls at Fort Sill in cast pellets of rough-legged hawks, *Buteo lagopus*, during a migratory influx of these and other buteos. Documented evidence of this vole population later was obtained by J. D. Tyler. While investigating the unusual sighting of a black-shouldered kite, *Elanus caeruleus*, on the east range of Fort Sill in March 1983, Tyler examined three of the raptor's cast pellets and found them to contain vole skulls (Andrew *et al.*, 1983).

The occurrence of *M. ochrogaster* in southwestern Oklahoma appears to represent a relictual population. Prairie voles are known from early Holocene and late Pleistocene fossil faunas located farther to the south and west in Texas (Graham, 1987), indicating that some limiting factor, such as the availability of suitable habitat, forced the withdrawal of this species northward. Intense seasonal climate fluctuation (Dalquest *et al.*, 1969; Graham, 1987), for example, could have resulted in increased aridity and grassland regression.

Several other studies have been conducted on the prairie vole and its natural history and population characteristics. The significance of the current study is that it is focused on a relict population of this species.

Microtus ochrogaster is a robust rodent with a pelage that has been described as being grizzled grayish brown dorsally and ochraceous ventrally (Jones *et al.*, 1983). It has a relatively stocky build, and short legs, ears, and tail. The tail is darker dorsally than ventrally, the eyes are small, and the snout appears blunt. These voles usually have five plantar tubercles on the soles of the hind feet as contrasted with six tubercles throughout the rest of the genus *Microtus* with the exception of the subgenus *Pitymys* (Johnson and Johnson, 1982). Also, the prairie vole has six mammary glands, two pair inguinal and one pair pectoral, rather than the typical four pair (two inguinal, two pectoral) of most microtines (Carleton, 1985), and the two inguinal pair in *Pitymys*.

The skull is high and narrow (Jones *et al.*, 1983), and the cheekteeth are characteristically prismatic and hypsodont (Carleton, 1985). In the subgenus *Pitymys* (including *M. ochrogaster* according to some authors), the aspect of the dentition that is most diagnostic is the lower first molar (Repenning, 1983). The occlusal surface of this tooth consists of the anteroconid complex, two confluent triangles, three closed triangles, and a posterior loop. All other voles of the genus *Microtus* have four or more closed triangles anterior to the posterior loop on m1 (Zakrzewski, 1985).

Anderson (1985) stated: "There is considerable uncertainty about the affinities of species of *Pitymys*, *Neodon*, and *Pedomys* with each other and with other species of *Microtus*." *Microtus ochrogaster* has been placed by some workers (Hall, 1981, for example) in the monotypic subgenus *Pedomys*.

Choate and Williams (1978) compared 13 Great Plains populations of prairie voles representing three of the six nominal subspecies of the species. Based on statistical analyses of morphometric data, they concluded that all plains populations should be assigned to *Microtus ochrogaster haydenii* (Baird, 1858) with the exception of *M. o. similis* Severinghaus (described in 1977) of the northwestern part of the range on the Great Plains. That subspecies was included in one of their 13 samples and part of another. The population of *M. ochrogaster* from Fort Sill was not studied by Choate and Williams (1978), who found crania of

TABLE 1.—*External and cranial measurements (mm.) of adult Microtus ochrogaster collected at Fort Sill, Oklahoma. Sample size (n) varies in cranial measurements due to damage to parts of some skulls. Except as noted, cranial measurements follow Choate and Williams (1978).*

Measurements	n	Mean	Minimum	Maximum	S.D.
Total length	51	142.8	131	154	7.07
Length of tail	51	32.7	26	43	2.88
Length of hind foot	51	19.2	18	21	0.80
Length of ear	51	12.5	10	15	1.00
Greatest length of skull	50	28.1	26.3	30.1	0.88
Zygomatic breadth	52	15.8	14.3	17.2	0.61
Postorbital constriction	53	4.3	3.9	4.8	0.22
Prelambdoidal breadth	49	11.1	10.2	11.7	0.32
Rostral length	52	8.6	7.8	9.4	0.39
Length of upper toothrow (*)	53	16.5	15.4	17.8	0.68
Length of lower toothrow (**)	53	6.6	5.9	7.5	0.34
Mastoidal breadth	48	12.7	11.6	13.5	0.38

*—Length from anterior base of incisor to posterior crown surface of corresponding upper third molar.

**—Length from anterior base of lower first molar to the posterior base of corresponding lower third molar.

prairie voles to be slightly larger in southern populations available to them than those to the north. However, they found no corresponding clinal relationship in external measurements. Individuals from the Fort Sill population of *M. o. haydenii* are small relative to those from the southern part of the range as reported by Choate and Williams (Table 1).

METHODS, MATERIALS, AND STUDY AREA

Microtus ochrogaster has been referred to as *Pitymys ochrogaster* by some authors based on the fossil record, primitive dental characters, and its apparent close relationship to other species of *Pitymys*, especially the woodland vole, *Microtus (Pitymys) pinetorum* (see Repenning, 1983; Zakrzewski, 1985). The fossil record indicates that both *Pitymys* and *Microtus* evolved from the Palearctic genus *Allophaiomys* (Chaline and Graf, 1988; Repenning, 1983). Many paleontologists (Repenning, 1983; Zakrzewski, 1985) have contended that the *Pitymys* group, including the subgenus *Pedomys*, evolved from *Allophaiomys* approximately one million years later than did the *Microtus* group, resulting in more primitive characters, especially in the dentition. Other workers (Chaline and Graf, 1988), however, have asserted that the group (including the genus *Microtus*) is monophyletic, although acknowledging the close relationship between the Nearctic *Pitymys* and *Pedomys* (both of which Chaline and Graf regarded

as subgenera of *Microtus*) based on both electrophoretic and morphologic characters. Inasmuch as the phylogeny of these groups is not entirely clear, and this study does not address systematic relationships, a conservative approach is taken by referring to the prairie vole simply as *Microtus ochrogaster*.

All mammalian nomenclature follows that of Jones *et al.* (1986). Names of birds and their seasonal status follow Tyler (1979) and the American Ornithologists' Union (1983) *Check-list of North American Birds*. The primary bird key used for identification was that of Scott (1983). Herpetological names and identification keys are taken from Conant (1975). Botanical keys used were Gould (1978), Irwin and Wills (1983), Little (1981), McCoy (1976, 1978), and Waterfall (1979).

Trapping Methods and Analyses

Voles were trapped on a regular basis from September 1986 to August 1987. A total of 71 *M. ochrogaster* was taken in 971 trap nights. External measurements, reproductive status, and other pertinent ecological data were recorded in field notes for all trapping periods. Other data are, represented in part by plant and vertebrate animal associates, summarized in Tables 2-4.

Victor rat traps, Victor mouse traps, Museum Special snap traps, and Sherman live traps (three by three by 12 inches) were utilized. Snap traps were baited with rolled oats, peanut butter, or pecan nut meats. Sherman traps were baited with rolled oats.

All specimens taken were prepared as standard museum skins accompanied by skulls, and have been deposited in the Collection of Recent Mammals, Midwestern State University, Wichita Falls, Texas. In contrast, many other workers have live-trapped *M. ochrogaster*, toe-clipped them, and recorded multiple catches of the same individuals. Typically, traps used in these studies were spaced 15 meters or 20 to 30 feet (six to nine meters) apart (Fitch *et al.*, 1984; Martin, 1956). During the course of this study, traps most often were placed in transects with a spacing of five meters between them.

The number of voles trapped before a major snowstorm in January 1987 was compared statistically to those trapped afterwards to determine any significant effect of the cold and wet weather. The same comparison was used to evaluate the population of *Sigmodon hispidus* before and after the snowstorm. Student's *t*-test was employed at a confidence limit of 95 percent, comparing numbers of each species when the null hypothesis for

TABLE 2.—Common herbaceous vegetation associated with habitat of prairie voles on the east range of Fort Sill, Oklahoma in 1986-87. Woody vegetation is not included as voles were seldom found in such associations.

Species		Vernacular name
	Grasses	
<i>Bromus</i> sp.		Brome grasses
<i>Aristida</i> sp.		Three awn grasses
<i>Chloris</i> sp.		Windmill grasses
<i>Bouteloua barbata</i>		Sixweeks gramma
<i>Bouteloua curtipendula</i>		Sideoats gramma
<i>Bouteloua gracilis</i>		Blue gramma
<i>Bouteloua hirsuta</i>		Hairy gramma
<i>Buchloe dactyloides</i>		Buffalo grass
<i>Panicum virgatum</i>		Switchgrass
<i>Andropogon gerardii</i>		Big bluestem
<i>Andropogon saccharoides</i>		Silver bluestem
<i>Andropogon scoparium</i>		Little bluestem
<i>Sorghum halapense</i>		Johnson grass
<i>Sorghastrum nutans</i>		Yellow indian grass
	Forbs	
<i>Delphinium virescens</i>		Prairie larkspur
<i>Baptisia</i> sp.		Indigo plant
<i>Oenothera serrulata</i>		Day-primrose
<i>Monarda</i> sp.		Horsemint
<i>Castilleja indivisa</i>		Scarlet paintbrush
<i>Proboscidea louisianica</i>		Devils claw
<i>Engelmannie pinnatifida</i>		Cut-leafed daisy
<i>Rudbeckia amplexicaulis</i>		Cone-flower
<i>Helianthus</i> sp.		Sunflowers
<i>Coreopsis grandiflora</i>		Golden-wave
<i>Thelesperma filifolium</i>		Thelesperma
<i>Cirsium texanum</i>		Texas thistle

each test was that there was no difference in size of populations preceding and following the storm.

Terrain

Fort Sill Military Reservation is a United States Army post comprised of 98,000 acres (39,660 hectares), which was established in 1869 by General Philip Sheridan in what was then Indian Territory. It includes a portion of the Wichita Mountains on its west range and an extensive grassland to the east. Although there are many different habitat types on the post, the east range (east of Main Post and East Cache Creek) was described as mixed-grass prairie by Blair and Hubbell (1938).

TABLE 3.—*Avian associates of prairie voles observed on the study area, Fort Sill, Oklahoma. Waterfowl were omitted from this tally.*

Species (status)	Vernacular name
<i>Cathartes aura</i> (S)	Turkey vulture
<i>Elanus caeruleus</i> (**)	Black-shouldered kite
<i>Ictinia mississippiensis</i> (S)	Mississippi kite
<i>Circus cyaneus</i> (W)	Northern harrier
<i>Parabuteo unicinctus</i> (**)	Harris' hawk
<i>Buteo swainsoni</i> (S)	Swainson's hawk
<i>Buteo jamaicensis</i> (*)	Red-tailed hawk
<i>Buteo regalis</i> (W)	Ferruginous hawk
<i>Buteo lagopus</i> (W)	Rough-legged hawk
<i>Falco sparverius</i> (*)	Kestrel
<i>Falco mexicanus</i> (W)	Prairie falcon
<i>Colinus virginianus</i> (*)	Northern bobwhite
<i>Charadrius vociferus</i> (*)	Killdeer
<i>Zenaida macroura</i> (*)	Mourning dove
<i>Tyto alba</i> (*)	Barn owl
<i>Bubo virginianus</i> (*)	Great horned owl
<i>Strix varia</i> (*)	Barred owl
<i>Asio flammeus</i> (W)	Short-eared owl
<i>Chordeiles minor</i> (S)	Common nighthawk
<i>Sayornis phoebe</i> (S)	Eastern phoebe
<i>Tyrannus verticalis</i> (S)	Western kingbird
<i>Tyrannus tyrannus</i> (S)	Eastern kingbird
<i>Tyrannus forficatus</i> (S)	Scissortailed flycatcher
<i>Eremophila alpestris</i> (*)	Horned lark
<i>Hirundo pyrrhonota</i> (S)	Cliff swallow
<i>Hirundo rustica</i> (S)	Barn swallow
<i>Corvus brachyrhynchos</i> (*)	Common crow
<i>Mimus polyglottos</i> (*)	Northern mockingbird
<i>Lanius ludovicianus</i> (*)	Loggerhead shrike
<i>Spiza americana</i> (S)	Dickcissel
<i>Chondestes grammacus</i> (S)	Lark sparrow
<i>Passerculus sandwichensis</i> (W)	Savannah sparrow
<i>Ammodramus savannarum</i> (S)	Grasshopper sparrow
<i>Sternella magna</i> (*)	Eastern meadowlark
<i>Sternella neglecta</i> (W)	Western meadowlark

*—Resident.

S—Present in summer (also spring and autumn).

W—Present in winter (also spring and autumn).

**—Rare or accidental species for study area.

The east range consists of approximately 27,000 acres (10,900 hectares) and is used by military personnel for both maneuver and firing exercises. Two large pieces of real estate totaling about 4100 acres (1660 hectares) make up the actual artillery impact area on the east range. These are pounded to a tilled state by the impact of high-explosive projectiles. Approximately 12,000 acres

TABLE 4.—Mammal, reptile, and amphibian associates of prairie voles that were trapped (*) or observed on the study area, Fort Sill, Oklahoma.

Species	Vernacular name
Mammals	
<i>Didelphis virginiana</i>	Virginia opossum
<i>Blarina hylophaga</i> (*)	Short-tailed shrew
<i>Cryptotis parva</i> (*)	Least shrew
<i>Dasypus novemcinctus</i>	Nine-banded armadillo
<i>Sylvilagus floridanus</i>	Eastern cottontail
<i>Lepus californicus</i>	Black-tailed jackrabbit
<i>Chaetodipus hispidus</i> (*)	Hispid pocket mouse
<i>Reithrodontomys fulvescens</i> (*)	Fulvous harvest mouse
<i>Peromyscus maniculatus</i> (*)	Deer mouse
<i>Peromyscus leucopus</i> (*)	White-footed mouse
<i>Sigmodon hispidus</i> (*)	Hispid cotton rat
<i>Canis latrans</i>	Coyote
<i>Canis familiaris</i>	Domestic dog
<i>Procyon lotor</i>	Raccoon
<i>Mephitis mephitis</i>	Striped skunk
<i>Felis catus</i>	Domestic cat
<i>Odocoileus virginianus</i>	White-tailed deer
Amphibians and Reptiles	
<i>Bufo cognatus</i>	Plains toad
<i>Terrapene carolina</i>	Ornate box turtle
<i>Elaphe obsoleta</i>	Texas rat snake
<i>Pituophis melanoleucas</i>	Bullsnake
<i>Sistrurus catenatus</i>	Western massasauga

(4850 hectares) surrounding the impact area serve as a buffer zone and access to it often is denied due to firing exercises that render it unsafe. Within this buffer zone, a 2200-acre (890-hectare) tall-grass prairie preserve has been designated as protected from haying because of its uniqueness. This area is directly adjacent to the southern impact area so access to it is extremely limited. Although actually a mixed-grass prairie, there are large areas within this reserve that contain a preponderance of tall grasses (Fig. 1).

Microtus ochrogaster of Fort Sill's east range exists in a disturbed habitat. There are numerous paved roads, dirt trails, firebreaks, range shacks, and other facilities, and it is common for tracked or wheeled vehicles to negotiate roadless areas of the post during maneuver exercises. Martin (1956) found graveled and heavily used roads to be barriers rarely crossed by prairie voles. Grass fires are common in and around the impact areas in the summer months and during other dry periods. Also, the post wildlife staff executes controlled burns as part of a professional

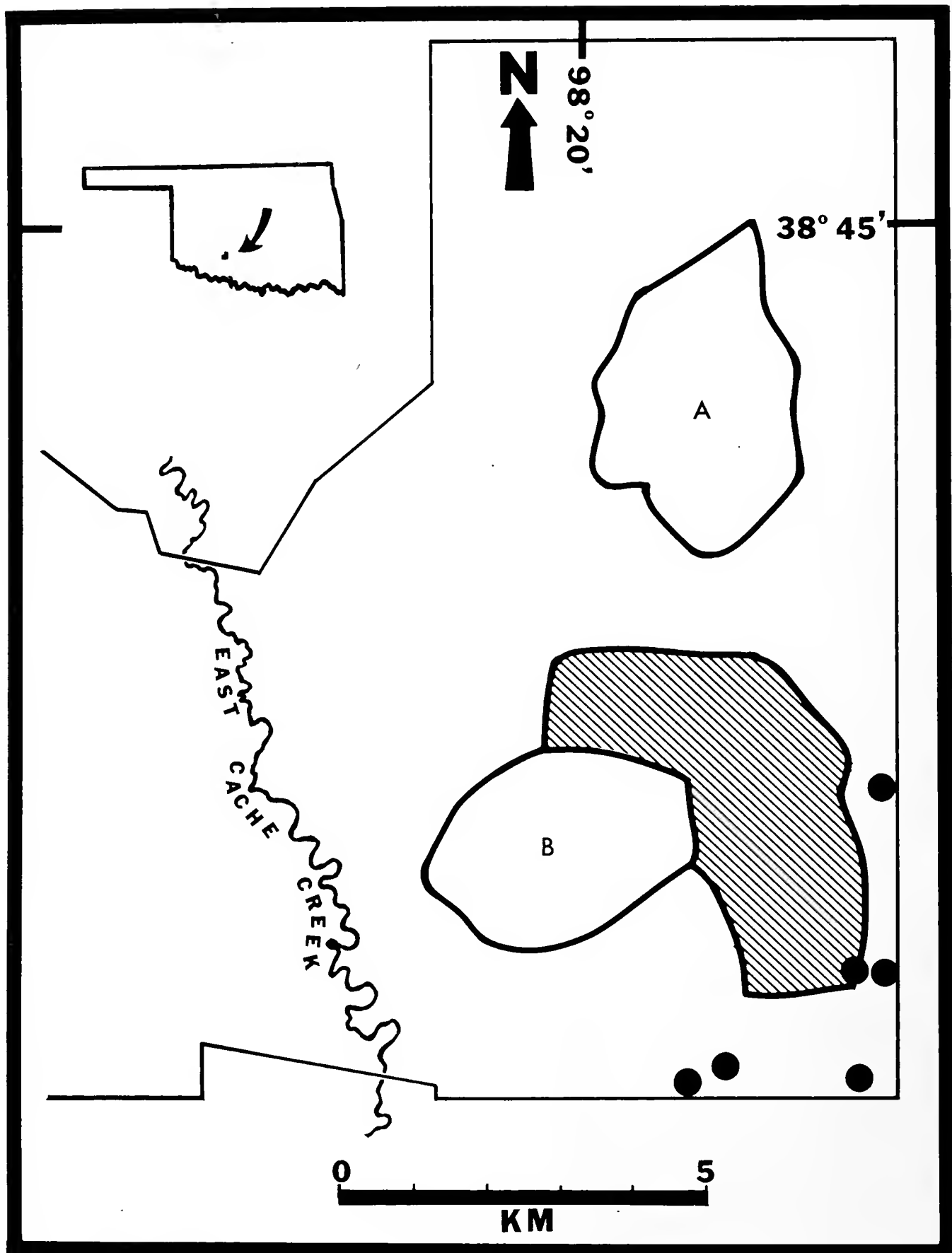


FIG. 1.—Study site, east range of Fort Sill, Oklahoma. Hatched area represents the Tall Grass Prairie Preserve. A and B indicate the north and south impact areas, respectively. Trapping locations are marked with black circles.

management plan. Approximately 10,000 acres (4045 hectares) are leased annually for civilian contract haying, which provides both revenue to the Government and reduces the possibility of uncontrolled fires.

Perennial and annual wildlife plantings are scattered across the east range. Perennials usually consist of low-growing, thorny

species such as Russian olive (*Elaeagnus angustifolia*), multiflora rose (*Rosa multiflora*), and honey locust (*Gleditsea tricanthos*). An interesting perennial plant that appears to have been introduced inadvertently is Osage orange (*Maclura pomifera*). These trees apparently grew from green posts used to build fences. A line of Osage orange trees occurs east from near East Cache Creek to the southeastern corner of Fort Sill. Brush and Osage orange trees also are present north intermittently along the east boundary fence for several kilometers, a total for both fences of almost six miles (9.5 kilometers).

Numerous small streams, drainages, and man-made ponds located on the east range support cottonwood (*Populus deltoides*), black willow (*Salix nigra*), soapberry (*Sapindus drummondii*), hackberry (*Celtis occidentalis*), plum (*Prunus* sp.), and elm (*Ulmus* sp.). The perennials provide cover and food for wildlife, especially white-tailed deer, *Odocoileus virginianus*, a species for which Fort Sill is managed intensively.

Annuals consist of alfalfa, hay-grazer, and milo. They usually are planted as part of a civilian contract with the United States Government to more completely utilize federal resources. It is a usual practice to either leave a portion of the crop for wildlife or plant seed-producing crops exclusively for wildlife.

Although these activities are all disturbances from a wild state, this habitat is not as disturbed as it would be had the land originally been homesteaded, plowed, or constantly overgrazed by the livestock of farmers attempting to derive a livelihood. All, or at least most, of this range never has been completely disturbed simultaneously. Perhaps because this land never has been extensively cultivated, it is occupied by *M. ochrogaster*.

The terrain on the east range is gently rolling and has been referred to by several generations of soldiers at Fort Sill as "the washboard" because of the difficulty of judging distance on this undulating grassland. The elevation above sea level is from 1302 feet (390 meters) to 1148 feet (350 meters) near East Cache Creek. The most common elevation of actual trapping transects was 380 meters.

Soils

Land use in Comanche County traditionally has been dryland farming as well as support of native and nonnative grasses for grazing of livestock (Mobley and Brinlee, 1967). Soils on Fort Sill were not mapped in the 1967 Soil Survey and its Supplement (Anonymous, 1982), but were mapped in a document of limited

distribution (about 25 copies) produced by the United States Department of Agriculture Soil Conservation Service for use in range management at Fort Sill (Anonymous, 1971). This conservation plan for Fort Sill included all soils on the east range except the actual impact areas. The major soils on the east range consist of Zaneis (prairie loam), Zaneis slickspots (loam to clay loam with dense clay subsoil), Lucien-Zaneis-Vernon complex (irregular mixture of loamy prairie and red clay prairie), and Foard and Tillman (hardland). These soils have the following potential plant productivity, measured in air-dried pounds per acre, during wet and dry years, respectively: 1) Zaneis, 4400:2700 pounds, 2) Foard and Tillman, 3300:1700 pounds, 3) Lucien-Zaneis-Vernon complex, 2500:1300 pounds, and 4) Zaneis slickspots, 1800:800 pounds (Mobley and Brinlee, 1967).

Climate

Fort Sill has a continental-type subhumid climate. Its weather patterns are considerably influenced by warm, moist air from the Gulf of Mexico and cool, marine air from the Pacific, and frigid, dry air from the Arctic (Mobley and Brinlee, 1967). Without the stabilizing influences of a seacoast, weather in southwestern Oklahoma is subject to extreme, abrupt changes.

According to the Air Weather Service Climatology Briefing of January 1987 (for the period of April 1939 through September 1986), January is the coldest month with a mean temperature of 33 degrees F (1°C), whereas July is the hottest month with a mean of 84 degrees F (29°C). The average rainfall at Fort Sill is 30.4 inches (77.2 centimeters) annually, with May the wettest month at 5.3 inches (13.5 centimeters), and January the driest month with 1.1 inches (2.8 centimeters). Mean annual snowfall is seven inches (17.8 centimeters), with heaviest snowfall usually in January and February (AWS Climatic Brief, 1987).

Vegetation

The plant community of Fort Sill's east range is a mixed-grass prairie (Table 2) with a preponderance of tall-grass species such as big bluestem (*Andropogon gerardii*), switch grass (*Panicum virgatum*), and indian grass (*Sorghastrum nutans*) in some areas (George Johnson, personal communication). Areas covered with dense stands of tall grasses and areas covered with grasses that tend to bunch at their bases (little bluestem, *Andropogon scoparium*) seem not to be favored by *M. ochrogaster*. Those

upland areas vegetated by the various grammas (*Bouteloua* sp.) and numerous forbs tend to be occupied by voles. *Microtus ochrogaster* never was trapped in sedges, in mesic habitats of swales, or in low-lying, grass-covered drainages. The ideal grass community for voles tended to be in areas with little or no bare earth visible from above, yet not more than six inches (15 centimeters) of basal cover and less than 30 inches (79 centimeters) total grass height. Meserve (1971) found that good grass cover increased trapping success of *M. ochrogaster* in western Nebraska. However, he also found no correlation between grasses known to be preferred vole food and the distribution of voles.

RESULTS AND DISCUSSION

Trapping Data

A total of 971 trap nights yielded 71 prairie voles, a success rate of 7.3 percent. Cotton rats, *Sigmodon hispidus*, were trapped 115 times during this same period, a success rate of 11.8 percent. Other species of this small mammal community trapped during the survey were *Chaetodipus hispidus* and *Reithrodontomys fulvescens*, each with six individuals (success rate 0.6 percent per species), and three shrews, two *Blarina hylophaga* and one *Cryptotis parva* (success rate of 0.2 percent and 0.1 percent, respectively). In all, 220 animals were trapped during the study, resulting in a success rate of 22.6 percent.

Five-meter spacing between traps in ideal habitat increased the success rate of trapping voles, which tended to be concentrated in isolated communities. Trap transects occasionally were run from less than ideal habitat through an area that appeared to be better habitat, and on to another area of less than ideal habitat. The small area of suitable habitat always yielded more *M. ochrogaster*, unless there was a large population of *Sigmodon hispidus* in the area. Cotton rats displaced voles from better to marginal habitats. This competitive exclusion has been documented by numerous authors (Baker, 1971; Fitch *et al.*, 1984; Fleharty and Olson, 1969; Glass and Slade, 1980).

With some minor exceptions, rolled oats were the superior bait for taking *M. ochrogaster*. Museum Special and Sherman traps were equally efficient in trapping voles as long as they were baited with rolled oats and placed near rodent runways. Use of Victor rat traps was discontinued early in the study because they often would be sprung without capturing a mammal. Use of

Victor mouse traps also was discontinued early because of their tendency to fracture the skulls of trapped mammals.

There were several instances when avian or mammalian predators in the area disturbed transects and carried off traps and their contents. Commonly, one or more adjacent traps simply would be missing. On one occasion, a transect had been set using 30 Victor rat traps. Four sequential traps were missing, but two of the four were located approximately 10 meters from the transect in a pile with what appeared to be the fur of *Sigmodon hispidus* and parts of the digestive tract of an herbivorous rodent. This was probably the work of a carnivore such as *Mephitis mephitis*, *Canis latrans*, or *Procyon lotor* (skunk, coyote, raccoon), which chews rather than bolts its food and, in at least this case, disliked the taste of the vegetation-packed digestive tract. The many avian predators were more suspect when traps simply vanished. Ants were a problem during the warmer months. They would quickly and systematically strip traps of bait and would destroy mammals caught in kill traps.

Much of the trapping was carried out during the nighttime hours, but enough data are available to conclude that in southwestern Oklahoma, *M. ochrogaster* maintains a similar periodicity to voles found elsewhere. Martin (1956) found this species to be primarily diurnal, especially in winter months, and Calhoun (1945) found it nocturnal in summer. Crepuscular activity tended to be the mode of vole activity on Fort Sill's east range. Specimens taken in live traps were either quite active, indicating that individual voles had recently entered the trap at dawn, or (especially during extreme heat or cold) dead, indicating that individual voles had been in the trap for a long period of time (probably since dusk the previous day). On several occasions traps were checked at dawn, mid-morning, and evening. Depending on season of the year, early morning and late evening seemed to be times of most vole activity. However, *M. ochrogaster* is active at virtually any hour of the day or night, again depending on the season.

Prairie voles were located in isolated colonies and were always found in an upland habitat. Various gramma grasses, *Bouteloua* sp., and silver bluestem, *Andropogon saccharoides*, in association with forbs, formed the preferred habitat. Reasons for favoring mid-sized grasses over the fairly abundant tall grasses may include: 1) *Sigmodon hispidus* favored the taller, coarser grasses and *M. ochrogaster* avoids cotton rats when there is contact (Fitch

et al., 1984; Glass and Slade, 1980); 2) the gramma grasses make a denser mat of detritus at the base of the plants, which enables the voles to construct above-ground runways that can be hidden from predators; and 3) some species of taller grasses, such as little bluestem bunch at their bases, leaving earth bare and thus exposing voles to predation.

Prairie voles never were taken in areas that seeped ground water or were immediately adjacent to standing water. Sites that had held populations of *M. ochrogaster* and were temporarily inundated due to heavy rains and snow melt contained no voles until the areas dried. By moving traps uphill, however, *M. ochrogaster* could be taken if the higher ground was not saturated with water, even if the vegetation was not ideal vole habitat. This indicated that at least some prairie voles went to higher ground to escape temporary high water due to runoff.

The winter of 1986-87 was unusually warm, but one snowstorm deposited three to four inches of wet snow on trapping sites at Fort Sill. As this snow began to melt and inundate burrows and rodent runways, most rodents either departed the immediate area or possibly succumbed to exposure. *Microtus ochrogaster* could still be taken on higher terrain that was wet but not submerged. *Sigmodon hispidus*, plentiful in the area prior to the snowstorm, virtually vanished. Cotton rats were not trapped in any numbers in the area until the following summer. Numbers of *M. ochrogaster* and *S. hispidus* trapped before and after the snowstorm were compared statistically (Student's *t* and *t*-adjusted tests, respectively) to verify any significant difference between them. There was no difference ($0.9 > P > 0.5$) between the numbers of *M. ochrogaster*, but there was a significant difference ($P < 0.05$) between numbers of cotton rats before and after the snowstorm. This tends to reinforce the idea that the generally subtropical *Sigmodon hispidus* is not nearly as cold tolerant as the more northern species, *M. ochrogaster*, especially when moisture is considered with low temperatures.

Predation

Extensive lists of predators on *M. ochrogaster* exist throughout the literature (Fitch *et al.*, 1984; Jones *et al.*, 1983; Martin, 1956; Meserve, 1971). Virtually all Great Plains carnivores have been reported to take *M. ochrogaster* at one time or another. Jones *et al.* (1983) surmised the prairie vole to be a “. . . most important prey species for many predators on the Northern Plains.”

On or near the east range of Fort Sill, *M. ochrogaster* has been documented as prey of numerous avian predators. Microtine skulls were observed in the cast pellets of a black-shouldered kite (Andrew *et al.*, 1983). The accidental appearance of this predator actually helped to first conclusively identify the population of prairie voles on the military reservation.

While conducting research on the nesting ecology of the loggerhead shrike, *Lanius ludovicianus*, J. D. Tyler (personal communication) observed the carcass of a prairie vole impaled on a thorn of an Osage orange tree, which was part of the larder of a loggerhead shrike. On 31 March 1987, a kestrel (*Falco sparverius*) was observed to take a small rodent (J. D. Tyler and S. Orr, personal communication). After some minutes of watching through binoculars, Tyler and Orr approached and the kestrel departed, leaving a decapitated adult *M. ochrogaster*.

Sam Orr bands raptors for the United States Fish and Wildlife Service and concentrates his efforts on Fort Sill. He estimates that in excess of 75 red-tailed hawks (*Buteo jamacensis*) resided on the east range during the winter of 1986-87, and that numerous other buteos such as rough-legged hawks and ferruginous hawks (*Buteo regalis*) also wintered there. Short-eared owls (*Asio flammeus*) are present during winter and have been observed hunting over the prairie of the east range.

George Johnson informed me that he had first become aware of the presence of the voles on the east range during a large influx of buteos, especially rough-legged hawks, during the early 1970s. This large influx of raptors at Fort Sill and the annual presence in large numbers of another raptor, the northern harrier (*Circus cyaneus*), may occur, at least in part, because of the presence of prairie voles. The wildlife staff at Fort Sill has, along with volunteers, conducted a census of the huge population of ground-roosting northern harriers on Fort Sill's east range during each of the last several winters. Census takers would surround the 2200-acre tall-grass prairie preserve and accurately count the harriers coming off the roost on a given morning. The total number of harriers present on four of the most recent occasions was in excess of 300, 200, 1000, and 700, respectively. The count of 1000 birds occurred in February 1987. Without considering the resident and wintering buteos (Table 3), barn, barred, and great horned owls (*Tyto alba*, *Strix varia*, *Bubo virginianus*) and various mammalian predators (Table 4), this huge number of wintering harriers would require a large prey population to maintain its numbers.

Microtus ochrogaster likely plays a major role as prey in conjunction with other high-density small mammals such as *Sigmodon hispidus*.

Fulk (1972) documented that shrews, especially *Blarina*, are known to prey upon voles in some circumstances. Although I have never witnessed this directly, one occurrence of indirect evidence was recorded. On 10 March 1987, one *Blarina hylophaga* was trapped along with 11 *M. ochrogaster* and six other small mammals. One of the voles taken in a Museum Special trap had numerous bite marks on its body. Bite marks were identical to the size and shape of the jaws of the trapped shrew. The vole evidently was not killed outright in the trap because some blood spots were located between the skin and the carcass, no doubt indicating that the shrew had attacked the much larger mammal while it was incapacitated.

Coyotes occur in fairly large numbers on the military reservation. Opportunistic in their food habits, these carnivores are quite adept at capturing rodents and, therefore, could be a substantial predator on *M. ochrogaster* at Fort Sill. As part of a white-tailed deer management plan, the wildlife staff at Fort Sill systematically hunts coyotes in an effort to reduce their predation on deer fawns. From 1977 through 1986, 399 coyotes were removed from the east range of Fort Sill by the wildlife staff (Jay Banta, personal communication).

Reproduction

Of the 71 specimens of *M. ochrogaster* taken on the east range of Fort Sill, 30 showed evidence of reproductive activity. Criteria used to determine evidence of reproduction for females were: 1) embryos implanted in the uteri (nine specimens), 2) obvious placental scars on the walls of the uteri (three specimens), and 3) obvious lactation (four specimens). A total of 15 females showed evidence of reproductive activity (one specimen was both lactating and had implanted embryos).

Testicular size was used to determine evidence of reproductive activity for males. Length and width measurements in millimeters were taken of the testes of each male vole. By multiplying the length times the width, an index was developed to determine if testes were enlarged enough for an individual to be considered reproductively active. A benchmark consisting of the two-dimensional surface area of 80 square millimeters was used to determine sexual activity. On that basis, 14 male voles were found

to be reproductively active, and 19 were found to be below the standard, thus recorded as inactive. Jameson (1947) reported that prairie voles with testes shorter than seven millimeters had microscopic tubules in the cauda epididymides that did not contain sperm, but those longer than seven millimeters had macroscopic tubules that did contain sperm. Hamilton (1937) found that testes smaller than eight by four millimeters lacked sperm in *Microtus pennsylvanicus*. My decision to include only those testes as reproductively active that were more than twice as large as those found to contain sperm in Jameson's (1947) study provides a conservative appraisal of reproductive activity in males for this population of *M. ochrogaster*.

Prairie voles were reproductively active throughout the entire survey period, September 1986 through August 1987, except for the hottest part of the summer (July and August). There was increased reproductive activity in spring and autumn, with the major period of reproduction being in spring. Similar findings are documented in the literature (Fitch *et al.*, 1984; Keller, 1985; Martin, 1956).

Richmond and Conway (1969) conducted extensive laboratory testing of the reproductive patterns of prairie voles and found gestation to be 21.5 days and that postpartum estrus occurs. The mean first litter was 2.54 young and this number steadily increased until the fifth litter when the mean was 5.0 young.

Litter size of the Fort Sill population of *M. ochrogaster* was based on the mean of all females that were gravid or that had obvious placental scars. The relatively small sample size ($n = 12$) required that all age classifications be considered together. The mean litter size of 3.0 young was based on a total of 36 fetuses and placental scars (29 and seven, respectively). Fetal counts ranged from one to six. This compares well with Jameson's (1947) data; he reported a mean litter size of 3.4 with extremes in fetal count of one and seven for 58 gravid females from Kansas.

Nest and Burrow System

Microtus ochrogaster digs and occupies burrows in hard loam, but these burrows usually are dug only after moisture makes the soil friable (Rose and Birney, 1985). Martin (1956) described underground nests as part of the characteristic runway system of *M. ochrogaster*. He characterized nests as being up to 200 millimeters in diameter and from 70 to 200 millimeters below the ground surface. The runway system of this and other voles has

received attention from numerous authors (Fitch *et al.*, 1984; Jameson, 1947; Jones *et al.*, 1983; Martin, 1956). Martin (1956) indicated that runways of *M. ochrogaster* in northeastern Kansas were long, crooked, and branching. He also stated that runways usually were under surface debris, approximately 50 millimeters in width, and only slightly cut into the bare ground. Although this generally describes the runways I observed at Fort Sill, two additional conditions frequently seemed to occur: 1) *M. ochrogaster* used the runways of *Sigmodon hispidus* when available, and 2) vole runways outside of ideal habitat often were short, disconnected segments of a runway system due to the lack of overhead cover, and because they were interspersed with burrows. The second situation occurred when *Sigmodon hispidus* was numerous and occupied the more favorable habitat in the immediate area, and when water inundated runways and forced at least part of the local *Microtus* population to drier terrain.

SUMMARY AND CONCLUSIONS

The population of *Microtus ochrogaster* at Fort Sill, Oklahoma, is a relictual one dating from earlier Holocene or late Pleistocene times. Fossil faunas containing prairie voles are known from a considerable distance west and south of the study area (Dalquest *et al.*, 1969; Graham, 1987). This marginal population does not seem to be expanding at present.

Prairie voles probably exist at Fort Sill because their habitat never was completely destroyed by farming and ranching practices. The east range of this military reservation is a disturbed habitat, but not nearly so disturbed as nearby areas subjected to homesteading and attendant agricultural practices.

Competition with *Sigmodon hispidus* has a negative impact on the population of *M. ochrogaster* at Fort Sill. Prairie voles are, however, much more tolerant of cold than are cotton rats. *Microtus ochrogaster* prefers habitat with a thick basal cover of vegetation, but when populations of *S. hispidus* are high, the voles may be displaced to less desirable habitat. Large numbers of raptors congregate in season on the east range of Fort Sill, perhaps partly as a result of availability of this prey species.

Museum Special traps and Sherman live traps were the most efficient means for taking prairie voles. The favored baits were meat of pecan nuts and rolled oats. *Microtus ochrogaster* was taken in similar numbers before and after a severe winter storm. *Sigmodon hispidus*, on the other hand, was present in large

numbers before the severe winter weather but was almost nonexistent afterwards.

Reproduction in *M. ochrogaster* occurred throughout the year except for the hottest and driest part of summer. Peak breeding activity occurred in spring and in autumn.

Microtus ochrogaster has been the subject of several natural history and population studies. Much information about its natural history is known. The importance of this study is the description of a population of this vole at the margin of the range of the species.

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KARYOTYPES OF FIVE SPECIES OF CUBAN LIZARDS

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In August 1988, we obtained several species of lizards from the Guantanamo Naval Base, Guantánamo (formerly Oriente) Province of Cuba. All but two individuals of these lizards were returned to the laboratory at Texas Tech University, and we prepared karyotypes from testes or bone marrow according to the procedures of Porter and Sites (1986). The remaining two lizards were karyotyped from tissue cultures (Sites *et al.*, 1979) in the laboratory of Michael W. Haiduk at Lamar University. The lizards studied included four species of the iguanid genera *Leiocephalus* and *Anolis*, and one species of the teiid genus *Ameiva*. All specimens are deposited as vouchers in the herpetology collection at Texas Tech University. The karyotypes of these species are described below.

Leiocephalus.—Representatives of two species of this genus both had 12 metacentric macrochromosomes, but differed in the number of microchromosomes. Three females of *L. carinatus* had a diploid number of 34, with 22 microchromosomes (Fig. 1A).

Five individuals of *L. raviceps* (four males and one female) were examined, and all had 18 microchromosomes and a diploid number of 30 (Fig. 1B, C). In the males (Fig. 1B), one microchromosome was considerably smaller than any of the others. Examination of more than nine diakinesis cells from three of the four males showed that this chromosome formed a heteromorphic bivalent with a larger microchromosome (Fig. 2A). Secondary spermatocytes had a haploid number of 15 (Fig. 2B). The single female examined of this species (Fig. 1C) had the same

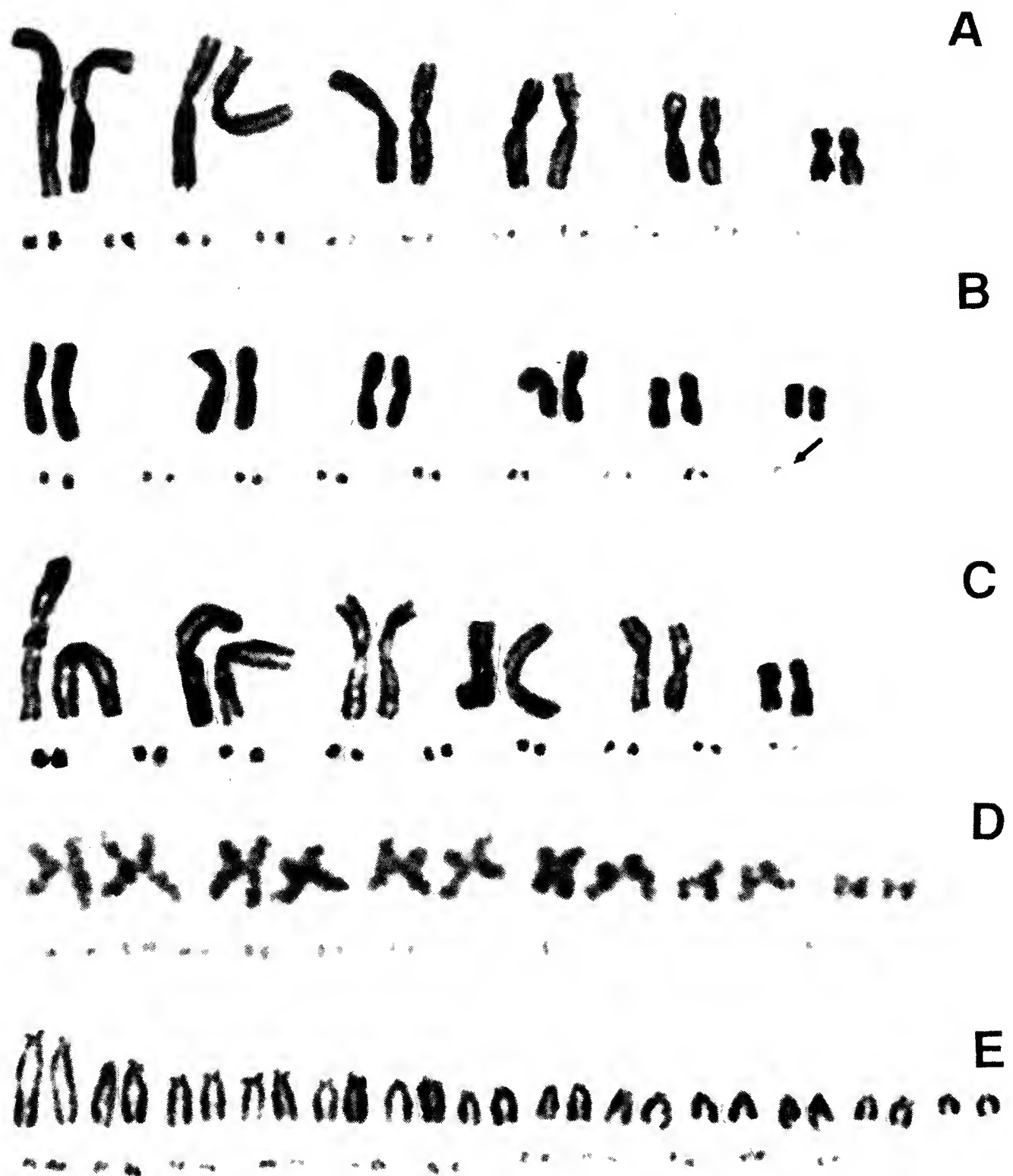


FIG. 1—A) Karyotype of female *Leiocephalus carinatus*; B) karyotype of male *Leiocephalus raviceps* showing the heteromorphic pair of sex chromosomes (arrow); C) karyotype of female *Leiocephalus raviceps*; D) karyotype of male *Anolis porcatus*; E) karyotype of female *Ameiva auberi*.

number of microchromosomes as the males, but did not have the unusually small microchromosome. These data suggest that *L. raviceps* has an XX/XY sex chromosome system, with the Y chromosome being minute, as has been reported in several species of the sceloporine genera *Uta* (Pennock *et al.*, 1969) and *Sceloporus* (Cole, 1971a, 1971b, 1978). The minute Y was seen in some of the secondary spermatocytes examined from males of this species. The remainder of the spermatocytes presumably possessed

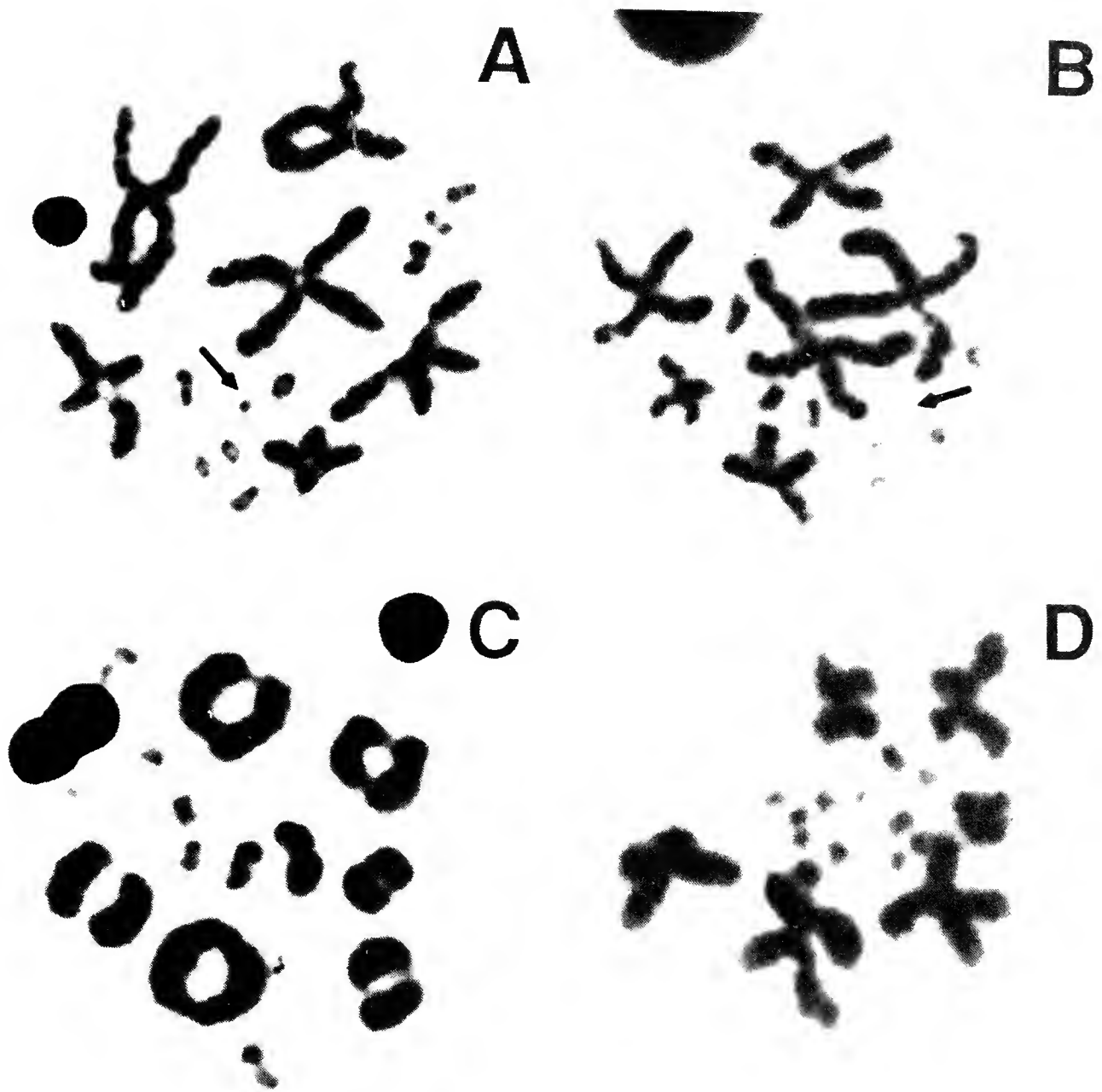


FIG. 2—Meiotic cells from male lizards. A) Diakinesis of *Leiocephalus raviceps* (the heteromorphic sex bivalent is indicated by an arrow); B) secondary spermatocyte from *Leiocephalus raviceps* (the presumed Y chromosome is indicated by an arrow); C) diakinesis of *Anolis homolechis*; D) secondary spermatocyte from *Anolis porcatus*.

the larger X chromosome, which is not distinguishable from the autosomal microchromosomes. Neither Gorman *et al.* (1967) nor Paull *et al.* (1976) mentioned sex chromosomes in other species of *Leiocephalus*, but slight heteromorphism in the microchromosomes easily might have been overlooked, and the heterogametic sex may not have been karyotyped in some cases.

Gorman *et al.* (1967) reported the karyotype of Haitian *Leiocephalus schreibersi* to consist of 12 metacentric macrochromosomes and 24 microchromosomes. Most iguanid genera that have been studied contain species with this 12 plus 24 karyotype, or a karyotype only slightly modified from that form. The 12 plus 24 karyotype is found in all of the major radiations of

iguanids, except the sceloporines, where all species (excluding the chromosomally diverse genus *Sceloporus*) have a 12 plus 22 karyotype. Some authors (Gorman *et al.*, 1967; Paull *et al.*, 1976; Bickham, 1984) have argued that the 12 plus 24 karyotype is ancestral for the family Iguanidae (and perhaps the entire suborder), although others (Cole, 1970, 1971*b*; King, 1981) have expressed differing opinions.

All *Leiocephalus* species karyotyped to date have 12 metacentric macrochromosomes, and the same pattern is found in other tropidurine genera such as *Tropidurus* and at least some members of the genus *Liolaemus* (Paull *et al.*, 1976; Peccinini-Seale, 1981). *Leiocephalus* karyotypes vary from the basic iguanid pattern only in the number of microchromosomes.

Paull *et al.* (1976) reported unpublished data of W. P. Hall from four unspecified species of *Leiocephalus*. Hall confirmed the *L. schreibersi* karyotype in at least one other Hispaniolan species, but "found representatives of the Cuban branch of the genus" to have only 20 microchromosomes. Paull *et al.* (1976) did not indicate which Cuban species were karyotyped by Hall, but based on the karyotype, it would appear that neither of the two species examined by us were included in Hall's studies.

Anolis.—We karyotyped two species of *Anolis*, and confirmed the karyotypes reported for these species by Gorman and Atkins (1968). Three male *A. homolechis* were examined, and all showed a $2n = 28$ karyotype with 14 biarmed macrochromosomes, and 14 microchromosomes. This karyotype was determined primarily from diakinesis cells, which had 14 bivalents (Fig. 2C).

One male *A. porcatius* had a $2n = 36$ karyotype with 12 biarmed macrochromosomes, and 24 microchromosomes (Fig. 1D). This karyotype is common among the alpha *Anolis* (Gorman *et al.*, 1967; Gorman and Atkins, 1968; Gilboa, 1975). No diakinesis arrays were found from this individual of *A. porcatius*, but haploid secondary spermatocytes showed the expected $n = 18$ karyotype (Fig. 2D).

Ameiva auberi.—We karyotyped one juvenile female of this species, and found a diploid number of 50, as in all other members of the genus that have been karyotyped (Matthey, 1933; Gorman, 1970, 1973; Gilboa, 1975). The 13 largest chromosome pairs in *Ameiva* are classified as macrochromosomes, although the size difference between macrochromosomes and microchromosomes is not particularly distinct. The karyotypes of *Ameiva* species differ only in the number of biarmed chromosomes.

Gorman (1970) hypothesized that the all-acrocentric karyotype of the mainland species *Ameiva ameiva* is ancestral for the genus. The same karyotype also is found in *A. exsul* from Puerto Rico (Gorman, 1970). However, other Caribbean *Ameiva* that have been studied have partially biarmed karyotypes, and the biarmed condition is apparently restricted to species from the West Indies (Gorman, 1970; Gilboa, 1975; Peccinini-Seale, 1981). In two Caribbean species (*A. dorsalis* from Jamaica and *A. maynardi* from the southern Bahamas), only the two largest pair of chromosomes are biarmed, whereas in the Hispaniolan species *A. chrysolema*, pairs 1, 5, and 8 are biarmed (Gorman, 1970).

We examined six cells from the Cuban *A. auberi*, and found that the five largest pair are biarmed, as well as three smaller pair of macrochromosomes, which we designated as pairs 7, 9, and 12 (Fig. 1E). Gorman (1970) suggested that the Caribbean radiation of the genus was derived from South American taxa having an entirely acrocentric karyotype, and that pericentric inversions arose in different combinations on the various islands. If this interpretation is correct, it would appear that *A. auberi* has rearranged its karyotype more extensively than other Caribbean *Ameiva* thus far studied.

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