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Microtus ochrogaster.

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Microtus ochrogaster (Wagner, 1842)

Prairie Vole

Hypudaeus ochrogaster Wagner, in Schreber, 1842:592. Type locality "America," probably from New Harmony, Posey Co., Indiana (Bole and Moulthrop, 1942:157).

Arvicola austerus Le Conte, 1853:405. Type locality Racine, "in Wisconsin."

Arvicola (Pedomys) cinnamonea Baird, 1859:541. Type locality "Pembina, Minnesota" [=Pembina, North Dakota?].

Arvicola (Pedomys) haydenii Baird, 1859:543. Type locality "Fort Pierre, Nebraska" [=Fort Pierre, Stanley Co., South Dakota].

Microtus (Pedomys) ochrogaster Allen, 1898:459, first use of name combination.

Microtus ludovicianus Bailey, 1900:74. Type locality "Iowa, Calcasieu Parish, Louisiana."

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Family Muridae, Subfamily Arvicolinae. The genus contains eight subgenera and approximately 47 species. *M. ochrogaster* is in the subgenus *Pedomys* (Ellerman, 1941; Hall, 1981). The following subspecies are recognized (Hall, 1981):

M. o. haydenii (Baird, 1859:543), see above.

M. o. ludovicianus Bailey, 1900:74, see above.

M. o. minor (Merriam, 1888:600). Type locality "Bottineau, Turtle Mt., Dakota" [=Bottineau Co., North Dakota].

M. o. ochrogaster (Wagner, in Schreber, 1842:592), see above.

M. o. ohionensis Bole and Moulthrop, 1942:155. Type locality "Symmes Creek, 2 miles north of Chesapeake, Lawrence County, Ohio."

M. o. similis Severinghaus, 1977:49. Type locality "KULR-TV Tower, Billings, Yellowstone Co., Montana."

M. o. taylori Hibbard and Rinker, 1943:256. Type locality "farm of H. H. Hildebrand, one and one-half miles north of Fowler, Meade county, Kansas."

DIAGNOSIS. Prairie voles (Fig. 1) may be distinguished from other arvicoline rodents (Hall, 1981) by their third lower molar that has three transverse loops and no closed triangles. Their third upper molar has two closed triangles. Their fur is long, coarse, and typically grayish brown. The tail usually is 26 mm in length. Difficulty occurs in differentiating *M. ochrogaster* and *Pitymys pinetorum* fossil remains, with the three most common criteria used: relative thickness of enamel, shape of m3, and the shortest distance between buccal reentrant angle three and lingual reentrant angle four. DeCoursey (1957) used M3 to separate sympatric *M. ochrogaster* and *M. pennsylvanicus*, but noted it was variable in *M. ochrogaster*.

GENERAL CHARACTERS. The dental formula of *M. ochrogaster* is 1/1, 0/0, 0/0, 3/3, total, 16 (Fig. 2). The teeth are among the simplest in the genus (Carleton, 1985). Ranges of external measurements (in mm) are (Hall, 1981): total length, 130 to 172; length of tail, 24 to 41; length of hind foot, 17 to 22; length of ear, 11 to 15; mass 37 to 48 g, but Martin (1956) reported adults up to 73 g. The pelage is usually grayish-brown above, with a mixture of black and brownish-yellow tips on longer hairs giving the dorsum a grizzled appearance (Mumford and Whitaker, 1982); however, the dorsum may be dark bister (Hall, 1981). Sides are paler than dorsum; venter is neutral gray or washed with whitish or pale cinnamon; tail is sharply bicolored. Mean cranial measurements (in mm) for males and females of *M. o. haydenii*, respectively, are: condylobasal length, 29.5, 29.3; zygomatic breadth, 16.6, 16.7; interorbital constriction, 4.0, 3.7; prelambdoidal breadth, 9.8, 9.6; lambdoidal breadth, 12.8, 12.8; length of maxillary toothrow, 7.2, 6.9 (Armstrong, 1972). Severinghaus (1981) demonstrated sexual dimorphism in the pelvic girdle of this species; however, utilizing 12 cranial measurements, Huggins and McDaniel (1984) noted dimorphism only for least interorbital width and length of mandibular toothrow. *M. ochrogaster* has no diastemal palate ridge (Carleton, 1985). No sexual dimorphism in size was noted between 181 males and 159 females that were field-caught in Indiana (Mumford and Whitaker, 1982), but it was noted in body mass among laboratory-raised prairie voles at 35 and 90 days of age (Dewsbury et al., 1980).

DISTRIBUTION. *Microtus ochrogaster* occurs from northeastern New Mexico, central Oklahoma and Arkansas, northern Alabama, and western West Virginia north and west to near Edmonton, Alberta (Fig. 3). A recently extinct race, *M. o. ludovicianus*, occurred in eastern Texas and western Louisiana (Lowery, 1974). Choate and Williams (1978) believe the type population of *M. o. taylori* has been extirpated and that *M. o. ochrogaster* is restricted to populations east of the central plains.

Recent range extensions in Arkansas (Moore and Heidt, 1981), Kansas, Oklahoma, and Colorado (Reed and Choate, 1988) have been reported. Clearing of forests has allowed this species to increase its distribution and abundance along the eastern margin of its range (Jones et al., 1983) with floodplains of rivers serving as dispersal routes in the Southwest (Reed and Choate, 1988). Railroad and highway rights-of-ways may serve as corridors for dispersal and genetic exchange throughout the range of the prairie vole (Moore and Heidt, 1981). However, interstate roadsides contribute less to dispersal of this species than of *M. pennsylvanicus* (Getz et al., 1987*b*).

FOSSIL RECORD. The genus *Microtus* probably originated in Asia with the first migration to North America across the Bering Land Bridge 1.8 mya (Zakrzewski, 1985). Zakrzewski also reported fossils of *M. ochrogaster* from >30 sites in 14 states, ranging in age from Pleistocene (Illinoian) to Holocene. Biochemical evidence (Chaline and Graf, 1988) contradicts the opinion that *M. ochrogaster* is the result of a separate evolution of *Allophaiomys* in North America. Most extra-limital records are in Oklahoma, New Mexico, and Texas (Smartt, 1977).

FORM. Molting occurs any time during the year, requiring 3 weeks for completion (Jameson, 1947). The first area of molting is pectoral, next extending ventrally cephalad and caudad, followed by lateral movement to legs and sides, with molting fronts typically meeting dorsally. Older prairie voles molt more slowly, in smaller areas, and they may grow irregular patches of hair 5 to 15 mm in length. Pelage color is similar in winter and summer, but winter fur is slightly darker and the belly is more buffy (Jones et al., 1983).

FIG. 1. Adult *Microtus ochrogaster* (originally published by Indiana University Press; photographed by J. O. Whitaker, Jr., with permission).

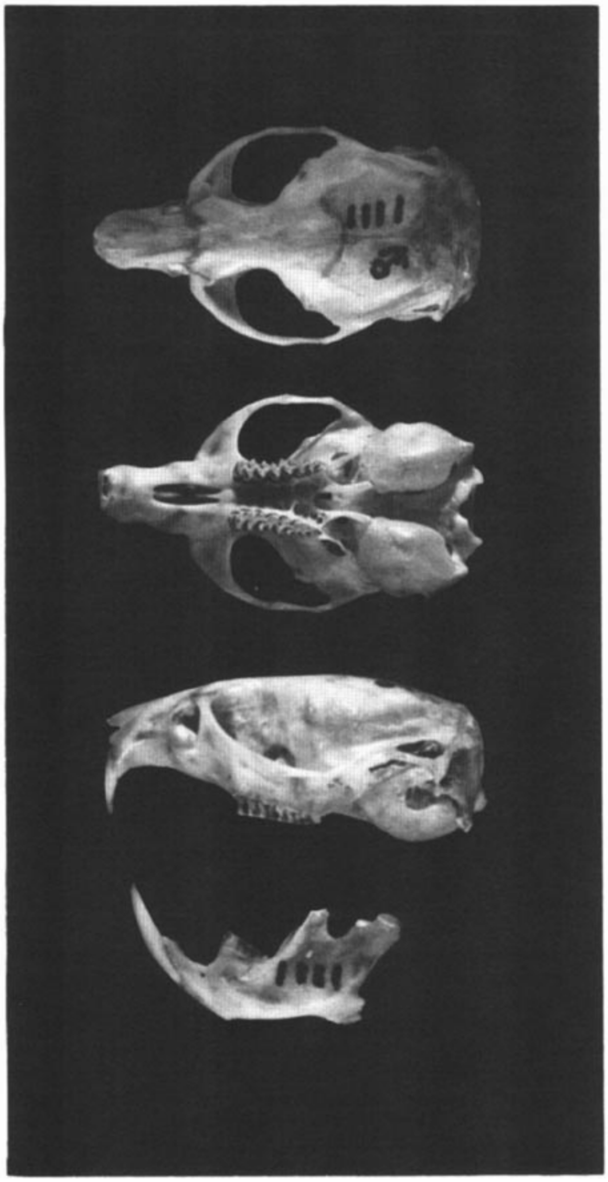

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of left mandible of *Microtus ochrogaster* (male, greatest length of cranium is 26.9 mm; Northwestern State University Vertebrate Museum 1111) from 1½ mi SW Burlington Junction, Nodaway Co., Missouri.

Color aberrations in the wild include xanthochromism (Getz and Pizzuto, 1987), melanism, albinism (Stalling, 1974), patches of silver hair, and silver venters (Mumford and Whitaker, 1982). In laboratory colonies, strains of albino, silver, white-footed (Richmond and Conaway, 1969*a*), smoky (Pinter and Negus, 1971), gray-eared (Semeonoff, 1972), and white spotting (Kruckenberg et al., 1976) have been noted. Xanthochromism (blonde) was found by Getz and Pizzuto (1987) to be a simple recessive trait.

Epidermal glands include a mean of 6.2 meibomian glands per eyelid set (Carleton, 1985), and poorly-developed flank glands (Jones et al., 1983). Three pair of mammae are present, one pair pectoral and two abdominal. The pectoral pair apparently are used only by females with more than four young (Fitch, 1957).

The villi and mucosal surface of the small intestine is typical of a herbivore (Carleton, 1985). Gross et al. (1985) noted significant increases in intestinal measurements at low temperatures and also with a high fiber diet, except for the length of the small intestine which decreased.

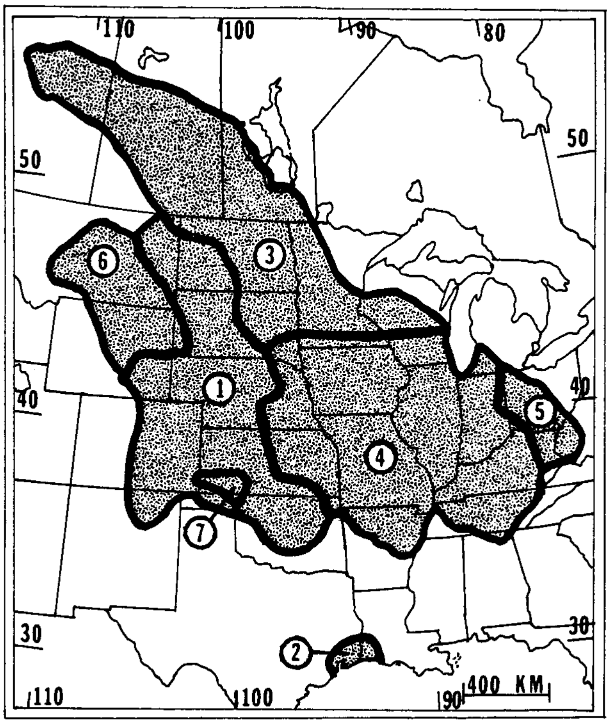

FIG. 3. Geographic distribution of *Microtus ochrogaster* in central North America (modified from Hall, 1981; Moore and Heidt, 1981; Reed and Choate, 1988): 1, *M. o. haydenii*; 2, *M. o. ludovicianus*; 3, *M. o. minor*; 4, *M. o. ochrogaster*; 5, *M. o. ohionensis*; 6, *M. o. similis*; 7, *M. o. taylori.*

The bacular stalk is broad; the greatest length is 3.2 to 4 mm, 1.6 to 2 times the greatest breadth, and 2.5 to 4 times the greatest depth. The center of the base is slightly depressed dorsally and flattened ventrally with lateral processes cartilaginous or with small ossifications (Carleton, 1985). The bacular shaft is straight with a slight terminal inflation. Papillae may occur on the rim of the glans penis. A single cone-shaped dorsal papilla is spined distally and dorsally. Urethral processes are wider than long, and divided into three blunt cones. Spines in the crater are widely spread and the ventral shield is unusually large (Hooper and Hart, 1962).

Accessory glands of males include a pair of preputial glands, irregular and lumpy vesicular glands, a little ampullary gland tissue, and four pairs of prostate glands (Carleton, 1985). The small anal and preputial glands, and no posteriolateral glands in this species is attributed primarily to their monogamous nature (Jannett, 1986).

The female uterine glands are straight and dilated at the end. The oviducts have an intramural portion within the wall of the uterine horn, a convoluted isthmus and a dilated ampulla that protrudes into the ovarian bursa (Janes, 1963). The vaginal orifice is sealed in sexually quiescent prairie voles, and occasionally it is sealed in pregnancy (Fitch, 1957).

FUNCTION. Of four rodent species studied in Kansas, *M. ochrogaster* had the lowest annual energy content per gram, showed monthly fluctuations in lipid content, and no seasonal variation in ash content (Fleharty et al., 1973). Metabolic and thermal conductance rates vary from 1.18 to 2.72 ml O_2 g^{-1} h^{-1} and 0.56 to 0.75 cal g^{-1} h^{-1} $°C^{-1}$, respectively, with variation depending on mass, acclimation, season, and test temperature (Wunder, 1985). Energy budgets for winter, summer excluding reproduction, and summer including reproduction are 21.52, 8.22, and 20.13 Kcal/day, respectively (Bradley, 1976). There is greater synthesis of fatty acids in the adipose tissue than in the liver (Baldner et al., 1984).

An adult can exist on dried food if provided 6 cc of water daily. There is an increased evaporative water loss of only 51% between 28 and 33°C, suggesting this vole is a poor evaporative cooler (Chew, 1951). *M. ochrogaster* drinks less, survives restriction better, utilizes higher molarities of salt water, and has a lower evaporative water loss than *M. pennsylvanicus* (Getz, 1963). Mean total body water is 62.2%, mean rate of water exchange is 11.7 ml/day, and the highest mean concentration of urine produced is 2,083.8 mOsm (Dupre, 1983).

Testosterone propionate injections, castration, and overwintering affects the mass of several glands including the adrenal, pituitary, thyroid, preputial, Harderian, and oral angle glands, ovaries, testes, and seminal vesicles (Beard, 1978). Intramuscular injections of estradiol benzoate and progesterone induce behavioral estrus (Gray and Dewsbury, 1973), and Hasler and Conaway (1973) noted vaginal and uterine epithelial changes in ovariectomized prairie voles injected with estradiol cyclopentylpropionate. Carter et al. (1986) found estradiol benzoate alone adequate to induce lordosis in ovariectomized and adrenalectomized females, but progesterone did not appear to be essential for female sexual behavior, and may be inhibitory. Reports of serum hormones include thyroxin averaging 4.8 μg/dl and adrenal 11 B-hydroxysteroids peaking during the autumn and winter (Seabloom, 1985).

Elevated hematocrits and decreased total plasma protein were reported for prairie voles in winter (Morton and Lewis, 1980), but Bopp and Platner (1966) noted elevated serum albumin levels in cold-stressed animals.

For anesthesia, Gier and Cooksey (1967) recommended diethyl ether or sodium pentabarbitol. Lepri et al. (1988) used ketamine-acepromazine and Kruckenberg et al. (1976) recommended any general anesthetic used for rats and mice. However, Baumgardner and Dewsbury (1979) found chloral hydrate to be unsafe.

ONTOGENY AND REPRODUCTION. Ovulation is induced about 10.5 h following copulation (Kruckenberg et al., 1976). The Bruce effect (induced abortion) has been seen in the laboratory with one prolonged exposure (Stehn and Richmond, 1975), with multiple short-term exposures (Hofmann et al., 1987), and under field conditions (Heske and Nelson, 1984). If a female is mated with two males, and each is allowed only one ejaculation, the male ejaculating last has a significant advantage with respect to litter composition (Dewsbury and Baumgardner, 1981).

Average pre-implantation and post-implantation mortality percentages range from 6.6 to 11 and 1.6 to 7, respectively. Average gestation lengths range from 20 to 22.8 days and mean litter size for field-caught animals is 3.5 while for laboratory raised animals is 3.9 (Nadeau, 1985). Richmond and Conaway (1969*a*) noted no effect of lactation on length of gestation. Litter size varies with maternal size and age, and season (Keller, 1985). Rolan and Gier (1967) noted that placentation sites are evenly spaced within each uterine horn regardless of embryo numbers. Placental scars disappear about 42 to 45 days following parturition (Corthum, 1967), with scar counts agreeing well with known litter size (Martin et al., 1976).

The reproductive season continues throughout the year (Keller, 1985) with lowest levels of activity in December to January and with highest levels of activity in May to October. Specific peaks of activity depend on availability of moisture. Short photoperiod did not reduce fertility in adult males, but did in juvenile males, suggesting that short days may in part be responsible for decreased reproduction in autumn and winter (Nelson, 1985).

At birth, crown-rump length ranges from 30 to 35 mm, eyelids and external auditory meatuses are closed, pinnae are bent forward and attached to the skin anteriorly, and digits are 75% fused (Kruckenberg et al., 1973). Mass at birth averages 3 g for laboratory-born animals and 3.5 g for young of field-caught animals. Postnatal-development landmarks include: incisors emerge, day 1-2; brown fur appears, day 2; pinnae unfold, day 2-3; crawl, day 4-5; eyes open, day 5-10; eat solid food, day 10-14; weaning, when weight between 11.9-18.4 g; first molt begins, day 21-28; second molt, day 40-84 (Nadeau, 1985). Daily weight increases to day 20 range from 0.61 to 0.83 g/day (Wunder, 1985). Nearly all growth is completed by 2 months (Martin, 1956), but the rostral length increases until the ninth month (Hoffmeister and Getz, 1968). Growth rates are highest in the spring, decrease with increased mass, are positively correlated with temperature, precipitation, and day length, but are negatively correlated with population size (Sauer and Slade, 1986).

Rarely are females perforate before 40 days of age. Martin (1956) however, reported a 26-day-old pregnant female and noted that during the summer in Kansas most females were pregnant before 6 weeks of age. Typically, being imperforate indicates an anestrous condition, but Richmond and Conaway (1969*b*) indicated that with experimenter-induced disturbances of anestrus-imperforate females, 52% became perforate. There are changes in the vaginal orifice and discharges during the reproductive cycle (Fitch, 1957). Females normally reach puberty at about 35 days and males in 42 to 45 days (Gier and Cooksey, 1967).

In males, pigmentation of the scrotum, and testis development are obvious by day 25 (Richmond and Conaway, 1969*a*). Jameson (1947) scored a male as fecund if the tubules of the cauda epididymis were observable through the scrotal skin. He also noted testis-size regression during 2 winter months, and their withdrawal into the body cavity. Sperm are found in the testes as early as day 31, and in the epididymis by day 33 (Richmond and Conaway, 1969*a*). The youngest male to sire a litter was 49 days old; however, Kruckenberg et al. (1976) suggested that for maximum breeding production, pairing should be made after 60 days of age. The spermatogenic cycle is 7.2 days in length (Schuler and Gier, 1976).

Estrus rarely occurs in the absence of an inducing stimulus; the two most effective stimuli are placement of females near males (71% induced) and direct contact with males (causing estrus in 83% of the females; Richmond and Conaway, 1969*b*). Females housed near males may remain in persistent estrus for 1 month. Typical duration of estrus is 24 to 48 h (Hofmann and Getz, 1986). Hasler and Conaway (1973) noted that a 72-h exposure to males was maximally effective in inducing estrus. However, Carter et al. (1987) suggested that direct physical contact with the male or chemical stimuli from the male are necessary to maintain behavioral estrus. Weanling females had the earliest vaginal opening when paired with adult males, next with nonlittermate males, and the latest when paired with littermate males (Hasler and Nalbandov, 1974). Adult females that have their vomeronasal organ removed, show impeded reproductive activity after pairing with males (Lepri and Wysocki, 1987). Postpartum estrus occurs; Richmond and Conaway (1969*b*) observed copulating before completion of all births of a litter.

Most prairie voles live one year in the field, but some have an inferred life span >650 days (Martin, 1956). Hofmann et al. (1987) reported survival of only 38 and 34% of trapped juvenile males and females, respectively, until they reached 30 days of age. In captivity, life expectancy is at least 16 months (Fisher, 1945). Getz (1965*b*) kept a captive-reared male and female for 35 and 27 months, respectively, as a mated pair, and they produced litters for 15 months.

ECOLOGY. Nearly every predator that is sympatric with *M. ochrogaster* has been reported to eat this vole (Eadie, 1944; Errington and Breckenridge, 1936; Kirkpatrick and Conway, 1947; Korschgen, 1957; Korschgen and Baskett, 1963; Martin, 1956). As a mammalian prey species in west-central Kansas, *M. ochrogaster* was second in importance only to the black-tailed jack rabbit (*Lepus californicus*; Wooster, 1939). Parasites include 30 species of mites, 4 ticks, 2 lice, 14 fleas, 1 acanthocephalan, 11 cestodes, 5 nematodes (Timm, 1985); 1 trematode (Rausch and Tiner, 1949), protozoan infections; 2 Mastigophora (Dunaway et al., 1968; Levine, 1965), and 2 Sporozoa (Ballard, 1968).

The interspecific interaction of the prairie vole and the cotton rat (*Sigmodon hispidus*) has been studied extensively. From stomach analysis in Kansas, it appears that competition exists for space rather than for food (Fleharty and Olsen, 1969). Terman (1974) noted that *Sigmodon* excluded and even killed and ate *M. ochrogaster* in confined areas, except where dense vegetation was provided. In Kansas field plots, Terman (1978) found that voles in the presence of *Sigmodon* showed late summer declines in population density, changed sex ratios, decreased survival rates, reduced mean residence times, and changes in spatial distribution and movements. However, Glass and Slade (1980) and Prochaska and Slade (1981) noted that the negative effect of *Sigmodon* on populations of *M. ochrogaster* was restricted to the reproductive season of *Sigmodon*, and they verified Terman's (1978) observation that the frequency of contacts was of primary importance in determining the severity of the effect. In the laboratory, Moroni (1975) showed *M. ochrogaster* to be dominant over *Peromyscus leucopus* with greatest dominance displayed during daytime and at nest sites. In Indiana, Whitaker (1967) was unable to detect competition of *M. ochrogaster* with *P. leucopus*, *P. maniculatus*, or *Mus musculus*; however, Abramsky and Tracy (1979) found *M. ochrogaster* and *P. maniculatus* to be strong competitors even though their niche overlap was small. *M. ochrogaster* and *P. maniculatus* overlap in 38% of their diets (Cook et al., 1982).

In laboratory studies, Rose and Spevak (1978) noted little aggressive exchange between *M. ochrogaster* and *Synaptomys cooperi*. In 0.8-ha enclosures, *S. cooperi* was dominant to *M. ochrogaster* if the former had the advantage of residency (Danielson and Swihart, 1987). If both species were attempting to secure new home ranges, *M. ochrogaster* was dominant. In spatial studies of these species in syntopy, Danielson and Gaines (1987) believed *M. ochrogaster* was selecting microhabitats that *S. cooperi* was not, and reported no competitive interference between these two species.

Where *M. pennsylvanicus* and *M. ochrogaster* are sympatric, the former is forced to retreat to moist marshy areas (Findley, 1954). In the laboratory, the prairie vole appeared to be dominant over *M. pennsylvanicus* (Getz, 1962); however, Miller (1969) reported the opposite. No evidence of detrimental interactions between field populations in Indiana was noted, with clear competition occurring only in fenced areas supporting high densities (Taitt and Krebs, 1985). Removal of either species from an area allows an influx of the other and *M. pennsylvanicus* is capable of invading and co-occupying an area with *M. ochrogaster*, but not vice versa (Klatt and Getz, 1987). Habitat segregation appears to occur due to the selection of *M. pennsylvanicus* for areas with taller vegetation and denser litter.

Prairie vole populations fluctuate widely with available moisture (Gier, 1967). Populations are highest in October and November (Getz et al., 1987*a*) or in April to June (Gaines and Rose, 1976). Maximum population densities may reach 1,060/ha (Crawford, 1971). Intervals between population-cycle peaks vary from 2 (French et al., 1976) to 4 years (Hamilton, 1937). Taitt and Krebs (1985) discussed the inability of penned prairie voles to regulate populations below limits set by starvation if dispersal is inhibited; however, in field populations living embryo counts were 25% lower during the period of a cyclic peak in multiparous females than they were during years of cyclic increase or decline (Keller and Krebs, 1970). In Kansas, litter sizes were no lower at peak density, but were significantly lower in the population decline (Rose and Gaines, 1978).

Aumann and Emlen (1965) believed that peaks of microtine densities were strongly correlated with soil-sodium levels, but Krebs et al. (1971) were unable to show this association in southern Indiana. In plots with differing food availability, Cole and Batzli (1978) and Getz et al. (1987*a*) noted sodium effects on breeding season length and amplitude of population fluctuations, but stated that soil sodium did not drive the population cycle. Using watered enclosures and enclosures supplied with bottles of water, Abdellatif et al. (1982) concluded that depression of summer reproduction was due primarily to the shortage of water as a plant stimulator. With supplemental feeding, Cole and Batzli (1978) concluded that available food influences the amplitude of population fluctuations, but believed that other factors must initiate the periodic declines. Similarily, McGovern and Tracy (1987) believed abiotic factors were important and not self-regulation in controlling growth of populations. After 14 years of population studies in three habitats, Getz et al. (1987*b*) concluded that distinct multiannual population cycles are not characteristic of this species and that most previous assumptions of multiannual cycles may be artifacts of short-term studies.

Larger adult voles (20–30% larger) during peak populations have been noted for *M. ochrogaster* (except Gaines and Rose, 1976). With the added importance of aggression, this larger size appears beneficial (Boonstra and Krebs, 1979).

The average population in Kansas has 45% males (range, 39.7–50.1%), with the lowest value obtained in April (Martin, 1956). From December to March, adults typically make up 86–96% of the population, but in June and November juveniles typically constitute 10% and subadults 25–30%. Low survival for males during the increase and peak phases of population cycles has been reported (Krebs et al., 1969).

The natural habitat of *M. ochrogaster* is the prairie, but within its range (Fig. 3) considerable differences are noted in dominant plants and available moisture. Habitats selected include: *Andropogon* and *Poa pratensis* meadows in Kansas (Brumwell, 1951); *Artemisia* and grass communities in Wyoming (Maxwell and Brown, 1968); grasslands dominated by *Festuca* and *Dactylis glomerata* in Indiana (Keller and Krebs, 1970); however, Getz (1985) reported large populations in several types of agricultural habitats. Kaufman and Fleharty (1974) captured *M. ochrogaster* in five communities (including riparian) in Kansas; they believe its presence in a habitat depends upon suitable cover for runways.

Dispersal has been viewed from perspectives such as genotype, population density, sex ratio, survival rate, and reproductive activity (Lidicker, 1985). However, using multivariate rather than univariate correlation analysis, Gaines and Johnson (1984) concluded that dispersal was density-independent as also has been reported by Getz et al. (1987*a*). Johnson and Gaines (1987) found a greater proportion of subadults among dispersers than among residents, greater fitness in emigrants than in residents, and that resident females benefited the most from living in a population where density had been reduced by dispersal. *M. ochrogaster* is considered a pre-saturation disperser with lactating females and subordinate males dispersing most readily (Lidicker, 1985). The importance of a narrow dirt road as a dispersal barrier in the movement of *M. ochrogaster* in different seasons was reported by Swihart and Slade (1984).

Size of home range in natural populations varies little (range, 0.11–0.22/ha; Harvey and Barbour, 1965; Martin, 1956; Meserve, 1971). However, penned populations in Illinois studied with radio-tracking and powdertracking produced mean estimates of only about 0.01/ha (Jike et al., 1988). A negative correlation between length of home range and population density, a positive correlation with the instantaneous rate of increase, and a negative correlation with herb biomass has been shown (Abramsky and Tracy, 1979). Home range sizes of adults and of subadults are positively associated with dispersal rates (Gaines and Johnson, 1982). Territoriality can be assumed, as laboratory animals will not tolerate crowding (Gier and Cooksey, 1967), and Crawford (1971) noted mass fighting in the field. With an increased population density there are shifts from pair territories to loose polygynous or promiscuous groups (Hofmann et al., 1987).

Martin (1961) reported evidence of *M. ochrogaster* preying on eastern pipistrelle bats (*Pipistrellus subflavus*) in a cave. The diet of caged *M. ochrogaster* included 79 species of prairie plants (Menhusen, 1963). From a year-long study of stomach contents, Zimmerman (1965) found *Poa compressa*, various roots, *Trifolium pratense*, and *Lespedeza* to constitute 15.8, 10.0, 9.7 and 6.7% by volume, respectively. He also noted 4.7% insect material; however, Fish (1974) believes this percentage should be considerably higher as they consume only the soft portions, thus making identification difficult. Using fecal-pellet analysis, Agnew et al. (1988) estimated that mixed arthropods composed from 0% in the spring to 44.3% in the late-summer diets in mixed-grass prairies in South Dakota. Stomach contents during June and July in Kansas contained stems and leaves of *Sporobolus asper*, *Kochia scoparia*, *Bouteloua gracilis*, *Bromus japonicus*, *Rumex crispus*, and *Digitaria sanguinalis*, with percentages varying according to the plant's availability (Fleharty and Olsen, 1969). Subterranean food caches contain primarily common seeds and underground plant parts (Jameson, 1947). Batzli and Cole (1979) found prairie voles to show high digestibility of *Medicago sativa* and grains, but on strictly a grass diet they lost weight and died. Digestion efficiency varies from 49.6% for *Poa pratensis* leaves to 74.4% for rat chow (Wunder, 1985), and from 73% in summer to 65% in winter for rat chow (Cherry and Verner, 1975). Depressed growth occurs with diets high in quercetin and tannic acid, and reduced intake occurs if the diet is high in quebracho (Batzli, 1985).

Prairie voles are a major problem where people plant trees; stem injury was reported in 14 species of hardwoods and 16 species of conifers (Jokela and Lorenz, 1959), with pines the most adversely affected. Bell and Dimmick (1975) used zinc phosphide to control populations of *M. ochrogaster* in tree plantations. Bromocresol green was used as a gastrointestinal stain to determine acceptance of treated bait (Nass and Hood, 1969). Heavy mortality occurs in fields where dieldrin is applied for insect control (Scott et al., 1959).

Laboratory management of prairie voles has been refined for >25 years (Mallory and Dieterich, 1985). Essentially all conventional methods for collecting and marking of small rodents have been employed to study populations of prairie voles, including the Burt multiple-capture trap (Getz et al., 1987*b*). Trap baits have varied widely, but Martin (1956) used a mixture of cracked corn, milo, and wheat. He believed the corn was important in winter to reduce trap mortality. Toe-clipping and ear-tagging are the most common means for permanent marking.

Estimations of populations typically have employed either snap-trapping (removal) or live-trapping (mark–recapture) techniques. Yang et al. (1970) used sequential trapping to compare live and snap-trap sampling for population estimation and found them closely related; however, juveniles were under-represented by both methods. Using computer simulation, Hilborn et al. (1976) examined the influence of five population parameters on censusing prairie voles.

BEHAVIOR. There are behavior-genetic mechanisms in population regulation in prairie voles (Tamarin and Sheridan, 1987). Levels of wounding (damaging bites) are comparatively great in winter, during periods of intense reproduction, among males, and among adults (Rose and Gaines, 1976). There is a relative absence of aggression between members of an established pair, yet high levels of aggression by either pair member toward strangers of either sex (Getz and Pizzuto, 1987). However, separation of pairs for 8 days, with the female living with a new male, breaks the old pair bond. Nonreproductive prairie voles in laboratory colonies live in communal groups (Thomas and Birney, 1979).

Reproductive behavior suggests monogamy because of failure of the males to demonstrate the Coolidge effect, strong pair bonds, equal sharing by parents in care of the young, older pups caring for neonate siblings, and because females do not show evidence of pair bonding until after mating (Getz et al., 1987*a*; Wolff, 1985). In the lab, females selectively associate and mate with dominant males (Shapiro and Dewsbury, 1986).

The copulatory pattern includes intra-vaginal thrusting, multiple intromissions and ejaculations, no lock, and typically males exhibit an average of two ejaculations before attainment of satiety (Gray and Dewsbury, 1973). However, Pierce et al. (1988) in 24-h observations noted a mean of 5.6 ejaculations over a period of approximately 16 h. Urine from estrous females does not decrease aggressive behavior among males (Stehn et al., 1976). Copulatory behavior using two males and one receptive female, shows no consistent differences in copulatory activity of dominant and subordinate males (Evans and Dewsbury, 1978).

The copulatory plug has a fibrous appearance when crushed (Richmond and Conaway, 1969*b*). The presence of a plug and no copulatory lock (Gray and Dewsbury, 1973) suggests stage 2 of Voss' (1979) evolutionary-reproductive sequence.

Unfamiliar, sexually inexperienced males interact with virgin females in a manner that permits physical contact, pheromone transfer, and the subsequent induction of female sexual behavior (Gavish et al., 1983). Autogrooming in females is proposed as the mechanism for transferring male-produced stimuli from the cage floor to the females' vomeronasal system (Witt et al., 1988). Low levels of olfactory investigation seen among sibling pairs may account for reproductive failure seen in such pairings (Getz and Pizzuto, 1987), but an 8-day separation is adequate to raise pairing and breeding success of siblings to that of total strangers. Littermates usually suppress growth and reproductive maturation of one another, but suppression disappears after physical contact with strangers (Batzli et al., 1977). Both sexes have the ability to discriminate mate odors from conspecifics in soiled shavings and urine (Newman and Halpin, 1988). Urine from virgin and pregnant females possesses a chemosignal that suppresses reproductive maturation in other females (Getz et al., 1983). Comparisons of the development of social behavior between siblings and non-siblings in *M. ochrogaster* and *M. pennsylvanicus* gave the former species higher scores for social interactions, with non-sibling dyads scoring the highest (Wilson, 1982).

In summer, when daytime temperatures are high, diurnal activity decreases; in winter, when nighttime temperatures are low nocturnal activity decreases (Madison, 1985). In the laboratory, males are active mostly at night with a major peak before midnight, and the pattern persists in either continuous light or dark. This species has labile nocturnal activity patterns, which are modified by environmental factors in the field (Calhoun, 1946).

Analysis of ultrasounds in five species of *Microtus* showed *M. ochrogaster* to be unique. Ultrasounds produced by pups greatly aids parents in finding them; few or no ultrasounds are produced by adults (Colvin, 1973). However, Lepri et. al. (1988) demonstrated significantly more ultrasonic vocalization by males than females and suggested that it served to communicate male gender and availability for reproductive behavior.

Non-social behavior includes locomotion, maintenance and comfort movements, digging, swimming, runway construction, and nest building (Wolff, 1985). The number of runways per meter of transect varies directly with population density (Carroll and Getz, 1976); thus, individual space may remain constant as population density varies. Evaporative water loss appears to be of little importance in influencing local distribution of runways (Getz, 1965*a*). Runways usually are bare and depressed in the soil surface due to repeated use (Jameson, 1947). Each runway system consists of a long, crooked central trunk with several branches (Martin, 1956). Burrow depth varies with soil type, but typically is at least 50 mm deep. Food or nest chambers are up to 200 mm in diameter, with tunnel lengths from the surface to the nest varying from a few millimeters to several meters. Typical subterranean nests are ellipsoidal (Fisher, 1945) with mean length of 180 mm, width of 150 mm, and depth of 100 mm; surface-nest dimensions vary only slightly. Nests typically consist of coarse dried grass on the outside, with finely shredded grass in the center. Nests often are constructed under boards or logs (Hahn, 1908).

GENETICS. Based on laboratory-raised animals from Tennessee, chromosome numbers are ($2n = 54$, $fn = 64$) and 40 of the autosomes are acrocentric, 12 are metacentric to submetacentric, with the X and Y chromosomes acrocentric (Hsu and Benirschke, 1971), however Modi (1987) reported $2n = 52$. Modi (1987) also noted that this species shows small size in the autosomal and X-chromosome centromeric C-bands, the Y chromosome is entirely heterochromatic, and that chromosome pair 20 shows geographic variability in possessing interstitial C-bands.

Genetic variation primarily has been approached using blood-protein electrophoresis with two or more electromorphs for each locus. The six known loci and the numbers of electromorphs are: transferrin, 4; leucine aminopeptidase, 2; 6-phosphogluconate dehydrogenase, 3; and esterases 1, 2 and 4, with 2, 2 and 2, respectively (Gaines, 1985). Early workers correlated electromorphs with population parameters such as size, growth rates, dispersal, or breeding activity. However, McGovern and Tracy (1985) demonstrated that exposure of prairie voles to different temperature regimes can change the mobility of electromorphs, thus casting suspicion on single-season studies or those conducted in the laboratory under constant temperatures (Gaines, 1985).

Other genetic aspects includes the demonstration by Nadler et al. (1978), that *M. ochrogaster* and *M. pennsylvanicus* have 80% of their loci with at least one allele in common and the report of Kruckenberg et al. (1973) that a long-term laboratory colony showed inherited polydipsia and muscular dystrophy.

REMARKS. The name *Microtus* is derived from the Greek words *mikros* (small) and *otos* (ear). The species name is also derived from two Greek words *ochra* (yellow-ochre) and *gaster* (belly). *M. ochrogaster* has been placed in the genus *Pitymys* by some authors.

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