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Home Range Overlap and Nest Cohabitation of Male and Female Prairie Voles

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ABSTRACT: The degree of association between male and female prairie voles *Microtus ochrogaster* was assessed using radiotelemetry. Nine sets of males and females caught together in live traps were fitted with transmitters and monitored for 3-4 days; an additional three sets of voles were radiotracked for 10 days. Eleven of the 12 male-female pairs remained together during the radiotracking period. The areas used by the male and female of each of these pairs overlapped greatly. Furthermore, each pair cohabited in a nesting burrow. On an average of 34.6% of the occasions when simultaneous readings were taken for a male and female, they were together in a nest. These results contrast markedly with field studies of *M. pennsylvanicus* and *M. montanus* which have revealed no nest cohabitation by adult males and females. The results of this study support laboratory evidence and live-trapping data suggesting pair-bonding in *M. ochrogaster*.

INTRODUCTION

Relatively little is known about the social organization of free-living populations of microtine rodents (Jannett, 1978, 1982; Madison, 1980a, b; Wolff, 1980; Wolff and Lidicker, 1981; Webster and Brooks, 1981). Because of the small size and secretive habits of these rodents, field observations of social interactions between recognizable individuals are difficult. Consequently, field evidence of social organization must be obtained by indirect means such as live trapping or radiotelemetry.

Expanding on ideas of Christian (1970), Getz (1978) speculated that microtine species that occur in extensive areas of continuous and relatively stable habitat would differ in social organization from those that occupy small, discontinuous and ephemeral habitats. He predicted that the basic social unit of the prairie vole *Microtus ochrogaster*, which originally inhabited large, contiguous prairie regions, would be a monogamous pair and its offspring, whereas the meadow vole *M. pennsylvanicus*, which originally occupied a patchy habitat (wet grassland), would have a nonmonogamous breeding system.

Laboratory observations and live-trapping data revealed behavior in *Microtus ochrogaster* consistent with the existence of a monogamous mating system (Thomas and Birney, 1979; Getz *et al.*, 1981; Gavish *et al.*, 1981). Getz *et al.* (1981) found that 13% of all adult captures in multiple-catch live traps were male-female double-captures. In 15.6% of these cases the same male and female were recaptured together during a 3-day trapping session; some pairs were recaptured up to 20 weeks later. However, such double-captures could either represent pairs that shared a home range or result from chance placement of traps in areas where the home ranges of two individuals partially overlapped.

In the present study, radiotelemetry was used to obtain more detailed information on the degree of association between free-living male and female *Microtus ochrogaster*. Presumed male-female pairs were monitored for home range overlap and nest cohabitation. The results are compared to studies of *M. pennsylvanicus* (Madison, 1980b; Webster and Brooks, 1981) and the montane vole *M. montanus* (Jannett, 1982), in which no nest cohabitation by breeding males and females was found.

METHODS

The study was conducted at the University of Illinois Ecological Research Area

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(Phillips Tract) located 10 km NE of Urbana, Illinois. Three specific sites within the area were used: a 1.0-ha alfalfa (*Medicago sativa*) field (AL), a 2.0-ha bluegrass (*Poa pratensis*) field (BGI) and a 0.8-ha bluegrass field (BGII). Small mammal populations on these three sites are routinely censused using multiple-catch live traps as part of a long-term study of microtine population dynamics. The AL and BGI fields are trapped monthly on a 10-m grid; BGII is trapped twice monthly on a 5-m grid. The vegetation typical of the study sites and the trapping methods are described by Getz *et al.* (1979).

The presumed pairs selected for radiotracking consisted of adult males and females that had been caught together in a live trap on the demographic grids. During October and November 1980 and November 1981 voles from nine male-female double-captures (two in BGI, four in BGII and three in AL) were fitted with transmitters. Each set of voles was monitored for 3-4 days. During June 1982 three additional sets of voles from AL were radiotracked for 10 days.

The radiotelemetry equipment (AVM Instrument Co., Dublin, Calif.) consisted of multiple-channel LA-12 direction-finding receivers with hand-held Yagi antennas and SM1 transmitters which emit a pulsed signal of a unique frequency. Each transmitter was soldered to a 1.4-v mercury battery and encased in dental acrylic. The collar was completed by bending the transmitter's insulated antenna wire into a loop and embedding its free end in the acrylic. The entire radio collar weighed approximately 2 g and was similar to those used on other small mammals (Banks *et al.*, 1975; Mineau and Madison, 1977; Madison, 1978, 1980b; Webster and Brooks, 1981).

The radios were placed on the voles in the field. The collars were positioned so that the transmitter was at the nape of the animal's neck and made secure by twisting the wire. The animals were then released at the site of capture. The amount of stress to the voles from the collaring procedure did not appear to be greater than that imposed by routine handling for the demographic study; there was no evidence of disruption of pregnancy in collared females. Upon completion of monitoring, the voles were live-trapped and the radiocollars removed.

Readings were usually taken at half-hour intervals during 4-6 hr blocks of time between 0500 and 2400 hr. The location of each collared vole was determined by triangulation based on two readings taken approximately 10 m apart by either one or two investigators. While locating a signal source, investigators moved slowly through the field and tried not to approach the vole too closely; preliminary observations indicated that an investigator could come within 1-2 m of an animal without influencing its movement.

The origin of a radio signal could be determined within an area of less than 1 m^2. Variation in signal intensity was taken as an indication that a vole was moving on the surface. The positions of active voles were recorded with reference to a 5-m grid. Whenever a male and female were in the same grid-square, the distance between them was estimated. When a vole was in an underground nest, the signal was weaker and less variable than when the animal was above ground. We located the burrows used by all collared voles; thus it was possible to determine when a signal originated from a nest.

Following the completion of radiotracking, further association between males and females was determined from live-trapping data. For pairs in BGI and BGII trapping data from the demographic grids (*see above*) were used. In AL the burrows of all breeding females (including those that had not been radiotracked) were located and four live traps were placed at the openings of each burrow. The burrows were trapped twice a week to determine which individuals were resident at each burrow.

RESULTS

Eleven male-female pairs remained together during the radiotracking period. Pairs 1-6 were tracked in October or November 1980, pairs 7-8 in November 1981 and pairs 9-11 in June 1982. The areas used by the male and female of each of these pairs overlapped broadly and each pair shared a common nest (Table 1). The remaining male and female (in BGI) were tracked to separate burrows 35 m apart within 4 hr of their release; subsequent live trapping suggested that each animal had a mate. Radiotracking of these voles was discontinued after 2 days.

Each pair of voles used only one nesting burrow except for pair 5 which appeared to be digging a new nest 7 m from their original nest site. Ten of the 11 males were never recorded at any burrow but that used by the female of the pair; male 3 spent approximately 4 hr in the nest of another female 50 m from his own nest. We also found 2-3 small surface nests of grass within the areas used by pairs 9, 10 and 11; the adults frequently occupied these nests during the day. For an average of 47.9% of the readings, males were located in the nests used by the females; for 13.5% of the readings the male was in the nest alone (Table 1). The male and female of a pair were found together in a nest on 34.6% of the occasions when they were both located (Table 1).

We estimated the area used by a female during the tracking period (which may not represent the entire home range) by connecting the outermost locations at which she was recorded. An average of 81.0% of the locations for males when they were active on the surface were within the range used by the female of the pair; 90.4% of all locations for males were within the females' ranges (Table 1). Most often, only one member of a pair was out of the nest at a time. When both animals were active above ground, they were in close proximity (within 2 m of each other) 36.1% of the time (Table 1).

The male of pair 3 and the female of pair 6 were accidentally killed at the end of the radiotracking period; the male of pair 7 was killed by a cat on the last day of radiotracking. Both members of the other eight pairs survived at least a week after the completion of radiotracking. Neither member of pair 2 was trapped at their shared burrow 2 weeks after radiotracking; subsequent trapping revealed that the male and female were both alive, but living separately in different parts of the study area (AL). The male and female of all other pairs apparently remained together until one member of the pair disappeared from the study areas and was presumed to have died. Live-trapping data suggest that pairs may have remained together for the following periods of time after we finished radiotracking: pair 1, 12 weeks; pair 4, 1 week; pair 5, 11 weeks; pair 8, 1.5 weeks; pair 9, 7 weeks; pair 10, 7 weeks; and pair 11, 8 weeks.

DISCUSSION

Although radiotracking of each pair in this study was of limited duration, there was an obvious, close association between male and female *Microtus ochrogaster*. Not only did the home ranges of the male and female overlap greatly, but they inhabited the same nest burrow.

The association of a male and female throughout the tracking period does not appear to have been merely the result of a male following a female in order to mate with her. Four of the females (Table 1) were pregnant and lactating and were, therefore, neither in nor approaching estrus. In addition, our observations of laboratory animals have shown that pregnant and lactating females are aggressive towards unfamiliar males. Therefore, a male probably would have had no opportunity to mate with these females during the tracking period. Three other females who were lactating had closed vulvae when collared, suggesting either that they had mated recently and had embryos that were too small to detect by palpation or that they were not in postpartum estrus. The remaining females were nonreproductive. Nonreproductive females come into estrus and mate within 24-48 hr of exposure to an unfamiliar male (Richmond and Conaway, 1969; Carter *et al.*, 1980). Thus, male-female association related only to mating would have been shorter than our tracking periods.

Facultative monogamy may occur at very low population density because of the limited chance of an individual encountering other conspecifics (Kleiman, 1977). Although there were no other *Microtus ochrogaster* in the vicinity of pair 5 in BGI, population densities in the other two study areas were not especially low. Density in

TABLE 1.—Summary of the results of radiotracking 11 pairs of *Microtus ochrogaster*. RC, reproductive condition of female (NR = nonreproductive, P = pregnant, L = lactating); N, number of readings for an individual; N_t, number of readings when both male and female were located; ♂♀B, % of N_t when the male and female were together in the nest burrow; ♂B, % of readings when the male was in the nest; ♂b, % of N_t when the male was alone in the nest; ♂♀<2m, % of surface readings when the male and female were within 2 m of each other (the number in parentheses = the number of readings when both voles were active on the surface); ♂w/i♀r, % of locations for an active male that were within the range of the female (the number in parentheses = the number of readings when a male was active); ♂W/I♀R, % of total male locations that were within the female's range

Pair	Field	Sex	RC	N	N_t	♂♀B	♂B	♂b	♂♀<2m	♂w/i♀r	♂W/I♀R
1	AL	♀	P,L	51	50	40.0	50.0	10.0	36.4(22)	92.0(25)	96.0
		♂		50							
2	AL	♀	L	65	63	55.6	46.7	0	0(10)	45.0(40)	70.7
		♂		75							
3	BGII	♀	NR	52	52	26.9	42.3	15.4	15.4(13)	66.7(30)	80.8
		♂		52							
4	BGII	♀	NR	50	50	66.0	76.0	10.0	50.0(2)	75.0(12)	94.0
		♂		50							
5	BGI	♀	L	62	37	8.1	34.5	13.5	84.6(13)	100.0(36)	100.0
		♂		55							
6	AL	♀	L	66	37	37.8	53.8	16.2	33.3(3)	94.4(18)	97.4
		♂		39							
7	BGII	♀	NR	60	56	30.4	41.1	10.7	66.7(30)	87.9(33)	92.9
		♂		56							
8	BGII	♀	NR	42	42	28.6	47.3	21.4	31.3(16)	79.3(29)	89.1
		♂		55							
9	AL	♀	P,L	148	96	39.6	43.4	12.5	29.4(17)	67.4(86)	81.6
		♂		152							
10	AL	♀	P,L	156	126	21.4*	34.1*	11.9*	40.0(65)	94.3(87)	96.2
		♂		132							
11	AL	♀	P,L	185	165	26.7**	57.6**	27.3**	10.3(87)	88.9(72)	95.3
		♂		170							
Means						34.6	47.9	13.5	36.1	81.0	90.4

* includes occupancy of a surface nest: ♂, ♀ in nest 12(9.5%), ♂ in nest 16(12.1%), ♂ alone in nest 4 (3.2%)
**includes occupancy of a surface nest: ♂, ♀ in nest 19(11.5%), ♂ in nest 42(24.7%), ♂ alone in nest 19 (11.5%)

BGII varied between 12/ha and 24/ha in October 1980 and was 14/ha in mid-November 1981. In AL, population density was approximately 35/ha in October 1980, 55/ha in November 1980 and 35/ha in June 1982. Thus, in this study males and females did not appear to remain together only because no other potential mates were available.

The use of space by male and female *Microtus ochrogaster* revealed by this study differs markedly from that of *M. pennsylvanicus*. Radiotelemetric studies of the latter species have shown no evidence of pair-bonding (Madison, 1980b; Webster and Brooks, 1981). Reproductive females occupied mutually exclusive home ranges, while breeding males had shifting home ranges that overlapped those of other males and of one or more females. Home range overlap between any male and female was short-lived; there was little contact between males and females except when a female was in estrus. During four breeding seasons Madison (1980b) did not find a single case of nest cohabitation by an adult male and female.

Jannett (1982) studied male-female association in field populations of *Microtus montanus* by tracking radioactively-tagged individuals that had overlapping home ranges. Males were often found in close proximity to active females whose nests were within their territories; some male-female dyads foraged together. However, during the breeding season there was no nest cohabitation by adult males and females, not even when a female was in estrus. Given the similarity of findings for *M. montanus* and *M. pennsylvanicus*, Jannett (1982) speculated that exclusion of males from the nests of breeding females might be a general characteristic of *Microtus*. The behavior of *M. ochrogaster* which differs from both of these species suggests otherwise.

The close male-female association revealed by radiotelemetry supports laboratory and live-trapping evidence for pair formation in *Microtus ochrogaster* (Gavish *et al.*, 1981; Getz *et al.*, 1981). Furthermore, the difference between this species and *M. pennsylvanicus* is consistent with Getz's (1978) hypothesis that these two species differ in social organization.

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