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DOES ACCESS TO FEMALES OR COMPETITION AMONG MALES LIMIT MALE HOME-RANGE SIZE IN A PROMISCUOUS RODENT?

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To maximize fitness, female mammals attempt to maximize offspring survival, whereas males attempt to mate with as many females as possible, which results in differential use of space. The relative influence of male competition versus access to females on space use by males has not been addressed theoretically or empirically. We conducted an experiment in which we manipulated total density, density of females, and density of males to determine relative influence of density of each sex on space use and overlap by male gray-tailed voles (*Microtus canicaudus*). Home-range size was correlated inversely with total density and was influenced separately by each sex. Home-range sizes of males were significantly smaller in high male–low female populations than in low female–high male populations. Males overlapped 4–5 females and 4–5 other males in populations with low densities of both sexes and high densities of both sexes. When sex ratios were skewed toward females, males still overlapped 4–5 females but only one other male. When sex ratios were skewed toward males, males overlapped only two females while overlapping three other males. Home-range size of a male does not appear to expand beyond an overlap with about five members of either sex. Thus, intrasexual competition with five males or overlap with five females appear to set upper limits to home-range size of male gray-tailed voles. We conclude that space use by males is influenced by intrasexual competition and access to females with an upper limit of overlap with either sex.

Key words: *Microtus canicaudus,* gray-tailed vole, home range, space use, density

Among mammals, females typically provide greater parental investment than males, which results in differential use of space (Emlen and Oring, 1977; Trivers, 1972). Due to high costs associated with pregnancy and lactation, females tend to compete with each other for food and space to rear offspring, whereas males compete with each other for access to reproductive females (Emlen and Oring, 1977; Trivers, 1972). This pattern of space use has been well-documented in small mammals (e.g., bank vole, *Clethrionomys glareolus*—Bujalska, 1994; grey-sided voles, *Clethrionomys rufocanus*—Ims 1987, 1988; meadow voles, *M. pennsylvanicus*—Madison, 1980, 1985; California voles, *M. californicus*—Ostfeld 1985, 1986, 1990; taiga voles, *M. xanthognathus*—Wolff, 1980, 1993). Among small mammals, males generally

provide minimal parental investment and thus can maximize their reproductive success by mating with as many females as possible. Because all males have this same strategy, considerable competition should occur among males for access to females. Thus, the two main factors that should limit reproductive success of a male mammal are number of females to which it has access and number of male competitors with which it interacts.

Male small mammals typically have home ranges that are twice as large as those of females, and their ranges overlap extensively with females and other males (Madison, 1985; Wolff, 1985), but factors that determine home-range size and overlap of males with respect to female density and dispersion are less clear. Ostfeld (1985, 1990) proposed that spacing behavior of

male microtine rodents is determined by spatial distribution of females. He suggested that males establish territories when females are spatially clumped and can be defended, but they overlap home ranges and "share" females when females are distributed evenly.

Results from experiments testing this hypothesis have been equivocal. Ims (1988) found that male grey-sided voles exhibited the greatest spatial overlap when females were clumped. However, Nelson (1997) found that spacing behavior of male field voles (*M. agrestis*) was the same irrespective of whether females were clumped or evenly distributed but was influenced by female densities. Nelson (1997) demonstrated that at high densities of females, males had smaller home ranges with less spatial overlap of other males than at low densities of females. Similarly, Jeppsson (1990) showed that male water voles (*Arvicola terrestris*) with access to females had significantly smaller home ranges than those without access to females. In addition, Nelson (1995) found that male home ranges were larger and more exclusive at low than high male density, but number of females overlapped by each male did not differ between low and high densities of males. These studies examined space-use responses of males to clumped versus widely dispersed females, low versus high densities of females, and low versus high densities of males, but they did not simultaneously test how number of male competitors versus number of potential female mates in a population influences home-range sizes and spatial overlap of males. The relative influence of male competition versus access to females on use of space by males has not been addressed experimentally.

Our objective was to determine if space use by males was influenced more by number of male competitors or by number of reproductive females in a population. We used the gray-tailed vole (*Microtus canicaudus*) as our behavioral model species. The gray-tailed vole is a typical herbivo-

rous grassland Microtus native to the Willamette Valley of western Oregon (Verts and Caraway, 1987). The breeding season extends from early March to late December (Wolff et al., 1994). Previous studies showed that home-range sizes of male gray-tailed voles decrease as total population densities increase (Wolff and Schauber, 1996; Wolff et al., 1994). Similar negative correlations between population density and home-range size of males have been documented in other arvicoline rodents (e.g., prairie voles, *M. ochrogaster*—Abramsky and Tracy, 1980; Gaines and Johnson, 1982; field voles—Erlinge et al., 1990). It is not known if the decrease in home-range size is due to increased male competition or higher densities of females. We attempted to distinguish between two alternative hypotheses to explain home-range size of male voles: 1) if the home-range size of a male were determined more by availability of females, its home-range size would be a function of the number of females to which it has access, or 2) if the home-range size of a male were determined by intrasexual competition, its home-range size would vary inversely with number of male competitors. The first hypothesis proposes that home-range sizes of males should decrease with increasing densities of females more so than with increasing densities of males, but the second hypothesis predicts that home-range sizes of males should decrease with increasing densities of males more so than with increasing densities of females.

To test these hypotheses, we measured the home-range sizes of male gray-tailed voles with respect to the relative number of male competitors and reproductive females in enclosed populations. Populations were manipulated to four combinations of density and sex ratio: equal sex ratios at low and high densities of both sexes, and sex ratios skewed towards either sex.

MATERIALS AND METHODS

Study site and experimental procedures.— Our experiment was conducted at Oregon State

University's Hyslop Farm, 10 km N of Corvallis, Oregon. Experimental units consisted of eight 0.2-ha (45 by 45 m) enclosures planted with several species of grass. All enclosures had similar vegetation and were considered homogeneous. Enclosures are constructed of sheet metal 90 cm high and buried 90 cm deep to contain the voles, and a 1-m strip was mowed bare along the inside of the fences to minimize its use by voles. In each enclosure, nine rows of nine trap stations were spaced 5 m apart for a total of 81 stations, with one Sherman live-trap at each station.

Six adult male and six adult female voles were placed into each of the eight enclosures in the beginning of May 1997, and population densities were allowed to increase until September 1997. Adult sex ratios were about equal throughout summer, with the lowest sex ratio being 1:1.7 ($n = 16$) in favor of females. Home-range sizes were calculated at low densities of both sexes (30–50 individuals of each sex/ha) using capture locations from 12 May to 4 July (8 weeks) and at high densities of both sexes (>150 individuals of each sex/ha) using capture locations from 28 July through 19 September (8 weeks). Mean total densities of both sexes combined in the enclosures were 60–100 voles/ha at low densities and >300 voles/ha at high densities; average densities in the experimental populations were comparable with moderate and high densities for free-ranging *M. canicaudus* (Wolff et al., 1996).

In September, one of two sex-ratio treatments was allocated randomly to each of the eight enclosures, providing four replicates of each treatment, for a completely randomized design with a one-way treatment structure. Population sex ratios were skewed either toward a high density of 25–32 males and a low density of 6–10 females (high males–low-females, HMLF), or a low density of 6–10 males and a high density of 25–32 females (low males–high females, LMHF). Mean total densities of both sexes combined ranged from 170–260 voles/ha in each of the eight sex-ratio treatment enclosures. Thus, densities of males and females were manipulated while total densities were held relatively constant. To initiate the sex-ratio experiment, females and males were removed from or added to previous populations such that the study animals would be spaced evenly throughout each enclosure. Home-range sizes were calculated using capture locations from 6 October through 28 November (8 weeks). All voles for which home-range sizes were calculated had an initial mass of 30–45 g and were in reproductive condition.

Trapping procedures.—Voles were trapped for 4 consecutive days at 2-week intervals for 7 months (8 weeks/period of home-range estimation). Traps were baited with oats and sunflower seeds and were either set in the evening and checked at sunrise or set before sunrise and checked midday, depending on the ambient temperature. All animals were ear-tagged for identification, and data recorded for each trapped animal included body mass, sex, reproductive condition of females, and trap location. Females were considered in reproductive condition if they were lactating or obviously pregnant. Voles were weighed to the nearest 1.0 g using Pesola scales. For the sex-ratio treatments, all juveniles were removed from enclosures to maintain skewed sex ratios and control densities.

Statistical analyses.—Spacing of animals in enclosures was determined by mark-recapture trap locations. Home-range sizes were estimated using the minimum-area-convex-polygon method for adult males and females caught more than seven times for 2 trap weeks, or more than five times for 3–4 trap weeks/period of home-range estimation. A single trap location that was >25 m from all other trap locations was considered either a sallie or a misread eartag and was discarded. To create an index of access to females and intrasexual competition per density and treatment, we calculated average number of female and male home ranges that each individual male home range overlapped. Two males were considered to have overlapping home ranges if their polygons overlapped or if they were captured at two or more of the same trap stations. Males were considered to overlap females if their polygons overlapped or if they were caught at one or more of the same trap stations. Home ranges were not calculated for animals that did not meet the minimum number of captures, but those animals were included in calculations of population densities and overlap. Past studies have shown that female gray-tailed voles maintain exclusive home ranges that are distributed evenly across enclosures (Wolff and Schauber, 1996; Wolff et al., 1994); therefore, we assumed that each male had relatively equal access to females.

Population growth was not controlled in the

low- and high-density populations as it was in the skewed sex-ratio populations. Therefore, we analyzed the low- and high-density populations separately from the sex-ratio treatments due to differences in experimental conditions. We used univariate (ANCOVA) and multivariate analysis of covariance (MANCOVA—SAS Institute Inc., 1996) with enclosures as replicates to compare differences in mean home-range size of males, mean number of males overlapped, and mean number of females overlapped by each male per enclosure per treatment. Variation in number of captures per individual was used as a covariate for home-range size. Home-range data were log-transformed before analysis, but back-transformed means were reported. All values were expressed as means and 95% *CI*.

RESULTS

The combination of mean home-range size of males, mean number of female home ranges overlapped, and mean number of male home ranges overlapped differed between low and high population densities (MANCOVA Wilk's lambda, F = 26.82; $d.f.$ = 3, 12; P = 0.0001). The combination of mean home-range size of males, mean number of females overlapped, and mean number of male home ranges overlapped also differed between the two sex-ratio treatments (MANCOVA Wilk's lambda, F = 115.27; $d.f.$ = 3, 4; P = 0.0002). Thus, ANCOVA was used to compare individual response variables of home-range size and male and female overlap between low and high densities and between sex-ratio treatments.

Home-range size.—Home-range sizes of males in low-density populations were significantly larger than those of males in high-density populations (ANCOVA, F = 72.98; $d.f.$ = 1,14; P < 0.0001). Average home-range sizes were 257.0 m² (95% *CI* = 159.3–354.8 m²) at low densities and 66.1 m² (95% *CI* = 54.5–77.6 m²) at high densities. As average population size increased by a factor of 3.6, average home-range size decreased by a factor of 3.8 (Fig. 1).

Home-range sizes of males in HMLF populations were significantly smaller than those in LMHF populations (ANCOVA, F = 6.54; $d.f.$ = 1, 6; P = 0.043). Average home-range sizes of males were 49.0 m² (95% *CI* = 37.7–60.3 m²) in HMLF populations and 85.1 m² (95% *CI* = 50.0–120.2 m²) in LMHF populations. Males in LMHF populations had home-range sizes that were 78% larger (95% *CI* = 46–117%) than in HMLF populations (Fig. 1).

Female home-range overlap.—Mean number of female home ranges overlapped by each male home range did not differ between low- and high-density populations (ANCOVA, F = 0.46; $d.f.$ = 1, 14; P = 0.5105). Males overlapped an average of 4.7 female home ranges (95% *CI* = 4.0–5.5) in low-density populations and an average of 5.3 female home ranges (95% *CI* = 5.0–5.6) in high-density populations (Fig. 1). Male home ranges overlapped significantly more female home ranges in LMHF populations than in HMLF populations (ANCOVA, F = 85.9; $d.f.$ = 1, 6; P = 0.0001). Males in LMHF populations overlapped an average of 6.0 female home ranges (95% *CI* = 4.8–6.4) but an average of only 1.8 female home ranges (95% *CI* = 1.4–2.3) in HMLF populations (Fig. 1).

Male home-range overlap.—Mean number of other male home ranges overlapped by each male home range did not differ between low- and high-density populations (ANCOVA, F = 0.41; $d.f.$ = 1, 14; P = 0.533). Male home ranges overlapped an average of 4.4 male home ranges (95% *CI* = 3.7–5.2) in low-density populations and an average of 4.0 male home ranges (95% *CI* = 3.7–4.4) in high-density populations (Fig. 1). Male home ranges overlapped significantly more home ranges of other males in HMLF populations than in LMHF populations (ANCOVA, F = 6.40; $d.f.$ = 1, 6; P = 0.045). Males in HMLF populations overlapped an average of 2.8 male home ranges (95% *CI* = 2.3–3.3) but an average of only 0.7 male home ranges (95% *CI* = −0.1–1.5) in LMHF populations (Fig. 1).
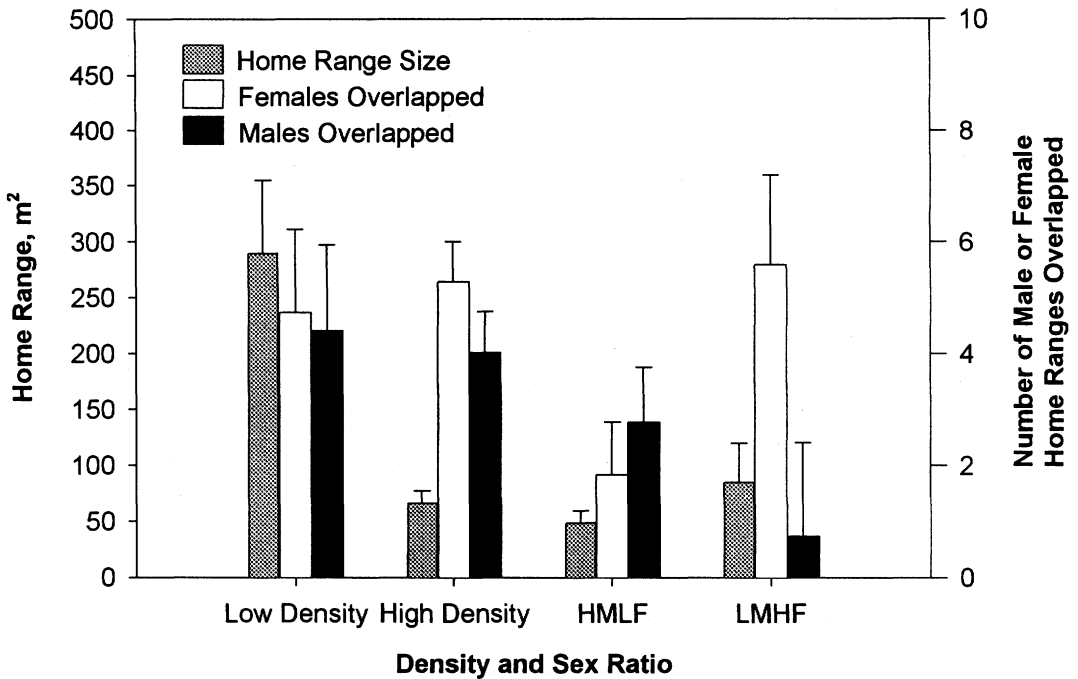
FIG. 1.—Mean (95% upper *CI*) home-range area of male gray-tailed voles (*Microtus canicaudus*) and number of male and female home ranges overlapped by males at four combinations of density and sex ratio (HMLF = high male–low female; LMHF = low male–high female) in eight enclosures at Hyslop Farm, Benton Co., Oregon, 1997.

DISCUSSION

Our objective was to determine if access to females or competition with males had the greatest influence on home-range size and space use of male gray-tailed voles. Results suggested that home-range size of males was influenced by a combination of density, access to females, and competition with males. Home-range size of male gray-tailed voles decreased significantly as total population density increased. However, average number of female and male home ranges that each male overlapped did not differ between populations of low and high densities with equal sex ratios. Males overlapped 4.0–4.4 other males and 4.7–5.3 females by having large home ranges at low densities (257 m²) and small home ranges at high densities (66 m²). That result demonstrated that home-range size of males was correlated negatively with density as predicted but did not indicate which sex had

the greatest influence on that relationship. Home-range size of males could have decreased due to increased access to high densities of females (hypothesis 1), or increased competition with high densities of males (hypothesis 2).

Results of the sex-ratio manipulations showed that home-range sizes of males were significantly smaller in populations with high densities of males than in populations with low densities of males. This result suggests that competition with males may limit a male's home-range size. In HMLF populations, each male home range overlapped only 1.8 females while overlapping 2.8 other males. The fact that males did not increase their home-range size after they overlapped about three male (but only about two females) supports the hypothesis that male competition may set the upper limit to use of space by males. Number of male competitors with overlapping home

ranges was fairly consistent, about three or four in low-density populations and in both treatments with 30 males.

If home-range size of males were determined mostly by competition with males, males in LMHF populations could have overlapped the home ranges of considerably more than five females while overlapping up to about four males. This was not the case. In LMHF populations, male home ranges overlapped about five females—the same number as in high and low densities—but only about one male. If male movements are limited by other males, males in LMHF populations (i.e., little intrasexual competition) could have increased their home-range sizes substantially, thus increasing their overlap of other males to the "upper limit" of about four, and increasing their overlap of females to even greater numbers. However, this did not happen. These data suggest that perhaps after a male gains access to about five females, it may not range farther, such that there also may be an upper limit of females that each male attempts to overlap. Thus, the hypothesis that female density influences space use by males also was supported.

Previous studies of small mammals have attempted to determine effects of female dispersion and density on space use by males (Agrell et al., 1996; Davies, 1991; Ims, 1988; Jeppsson, 1990; Nelson, 1997; Ostfeld, 1986,) and the effect of male density on space use by males (Nelson, 1995). Nelson (1995, 1997) found that male field voles had smaller and more exclusive home ranges at high than at low densities of females, and that males overlapped fewer other males at low than at high densities of males, similar to our results. Agrell et al. (1996) also found that male field voles overlapped fewer other males at high than low densities of females, and Jeppsson (1990) demonstrated that male water voles with access to females had smaller home ranges than males without access to females. However, these experiments did not test if number of potential mates or number

of male competitors plays a greater role in limiting use of space by males. Most theory on arvicoline spacing systems predicts use of space by males to be based on female dispersion and abundance (Bujalska, 1994; Ims, 1987; Madison, 1985; Ostfeld, 1985, 1990; Wolff, 1993; cf. Fortier and Tamarin, 1998). However, our results indicated that male intrasexual competition also influences movements of males. Our findings also demonstrated that there may be an upper limit of both males and females that each male will overlap, which is ultimately reflected in size of the home range.

According to evolutionary theory, males that provide minimal parental investment, as in most small-mammal species, should maximize their reproductive success by mating with as many females as possible (Trivers, 1972). However, attempts to mate with large numbers of females have two major costs, competition with other males and increased risk of predation, both of which limit movement and access to mates. In our study, maximum number of male home ranges that a given male overlapped was about four, regardless of number of females. Males apparently adjusted their home-range sizes in response to number of male competitors, presumably to minimize aggressive interactions. Thus, spatial overlap and competition with other males may have a high fitness cost and limit home-range size.

Male voles are typically more vulnerable to predators than are females (Korpimäki, 1985; Mappes et al., 1993), and male voles that are more active (Koivunen et al., 1996) or have larger home ranges (Norrdahl and Korpimäki, 1998) suffer greater mortality than males with smaller home ranges or that are less active. Thus, increased movement, activity, and use of large home ranges may increase risk of predation sufficiently to be a selective force for maintaining as small a home range as possible while still providing access to some mates.

Number of females that a male vole can effectively monitor and inseminate is not

known. Perhaps for a rodent with high reproductive rates (females in estrus every 21 days) and a 4-day estrous cycle, five females is an appropriate number for a male to monitor on a regular basis. Beyond these five females, male competition and risk of predation increase sufficiently that males maintain an optimal home-range size that provides maximum fitness benefits while minimizing costs of competition and predation. Reproductive success of males may be maximized by balancing breeding opportunities, reduced competition, and minimized risk of predation.

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LITERATURE CITED

ABRAMSKY, Z., AND C. R. TRACY. 1980. Relation between home range size and regulation of population size in *Microtus ochrogaster*. Oikos, 34:347–355.

AGRELL, J., S. ERLINGE, J. NELSON, AND M. SANDELL. 1996. Shifting spacing behavior of male field voles, *Microtus agrestis*, over the reproductive season. Annales Zoologici Fennici, 33:243–248.

BUJALSKA, G. 1994. Female and male territoriality in the bank vole. Pp. 56–69, *in* Animal societies: individuals, interactions and organizations (J. J. Jarman and A. Rossiter, eds.). Kyoto University Press, Kyoto, Japan.

DAVIES, N B. 1991. Mating systems. Pp. 148–169, *in* Behavioral ecology (J. R. Krebs and N. B. Davies, eds.). Oxford University Press, Oxford, United Kingdom.

EMLEN S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science, 197:215–223.

ERLINGE, S., I. HOOGENBOOM, J. AGRELL, J. NELSON, AND J. SANDELL. 1990. Density-related home range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. Journal of Mammalogy, 71: 597–603.

FORTIER G. M., AND R. H. TAMARIN. 1998. Movement of meadow voles in response to food and density manipulations: a test of the food-defense and pup-defense hypotheses. Journal of Mammalogy, 79: 337–345.

GAINES, M., AND M. JOHNSON. 1982. Home range size and population dynamics in the prairie vole *Microtus ochrogaster*. Oikos, 39:63–70.

IMS, R. A. 1987. Male spacing systems in microtine rodents. The American Naturalist, 130:475–484.

———. 1988. Spatial clumping of sexually receptive females induces space sharing among male voles. Nature, 335:541–543.

JEPPSSON, B. 1990. Effects of density and resources on the social system of water voles. Pp. 213–226, *in* Social systems and populations cycles in voles. (R. H. Tamarin, R. S. Ostfeld, S. R. Pugh, and G. Bujalska, eds.). Birkhaus-Verlag, Basel, Switzerland.

KOIVUNEN, V., E. KORPIMÄKI, H. HAKKARAINEN, AND K. NORRDAHL. 1996. Prey choice in Tengmalm's owls: preference of substandard individuals. Canadian Journal of Zoology, 74:816–823.

KORPIMÄKI, E. 1985. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. Annales Zoologici Fennici, 22:91–104.

MADISON, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. Behavioral Ecology, 7:65–71.

———. 1985. Activity rhythms and spacing. Pp. 373–413, *in* Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists, 8:1–893.

MAPPES, T., M. HALONEN, J. SUHONEN, AND H. YLÖNEN. 1993. Selective avian predation on a population of the field vole, *Microtus agrestis*: greater vulnerability of males and subordinates. Ethology, Ecology and Evolution, 5:519–527.

NELSON, J. 1995. Intrasexual competition and spacing behaviour in males of the field vole, *Microtus agrestis*, as revealed under constant female density and spatial distribution. Oikos, 73:9–14.

———. 1997. Determinants of male spacing behavior in microtines: an experimental manipulation of female spatial distribution and density. Behavioral Ecology and Sociobiology, 37:217–223.

NORRDAHL, K., AND E. KORPIMÄKI. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology, 79:226–232.

OSTFELD, R. S. 1985. Limiting resources and territoriality in microtine rodents. The American Naturalist, 126:1–15.

———. 1986. Territoriality and mating system of California voles. The Journal of Animal Ecology, 55: 691–706.

———. 1990. The ecology of territoriality in small mammals. Trends in Ecology and Evolution, 5:411–415.

SAS INSTITUTE INC. 1996. SAS/STAT user's guide. Version 6.12. SAS Institute Inc., Cary, North Carolina.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 597–599, *in* Sexual selection and the descent of man (B. G. Campbell, ed.). Adline, Chicago, Illinois.

VERTS, B. J., AND L. N. CARAWAY. 1987. Microtus canicaudus. Mammalian Species, 267:1–4.

WOLFF, J. O. 1980. Social organization of the taiga vole, *Microtus xanthognathus*. The Biologist, 62: 34–45.

———. 1985. Behavior. Pp. 340–372, *in* Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists, 8:1–893.

———. 1993. Why are female small mammals territorial? Oikos, 68:364–369.

WOLFF, J. O., AND E. M. SCHAUBER. 1996. Space use and juvenile recruitment in gray-tailed voles in response to intruder pressure and food abundance. Acta Theriologica, 41:35–43.

WOLFF, J. O., W. D. EDGE, AND R. BENTLEY. 1994. Reproductive and behavioral biology of the gray-tailed vole. Journal of Mammalogy, 75:873–879.

WOLFF, J. O., T. A. MANNING, S. M. MEYERS, AND R. BENTLEY. 1996. Population ecology of the gray-tailed vole, *Microtus canicaudus*. Northwest Science, 70:334–340.