

Space use and juvenile recruitment in gray-tailed voles in response to intruder pressure and food abundance

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We examined space use by female gray-tailed voles *Microtus canicaudus* (Miller, 1897) and recruitment of juveniles in response to relative abundance of food and increased intruder pressure following experimental removal of habitat. Our experiment indirectly tested the assumptions of the food-defense and pup-defense hypotheses for female territoriality. Following a 70% reduction in habitat, territories of females shrunk from ~50 m² to < 20 m² with no significant difference in pregnancy rates or overall juvenile recruitment compared to controls. Juvenile recruitment was not adversely affected by overall density or the numbers of males sharing a patch, but decreased significantly as the number of unrelated adult females sharing a patch increased. We did not measure infanticide directly, but the decreased rate of juvenile recruitment in the presence of adult females but not males suggests that pup mortality rather than food limitation contributed to reduced juvenile recruitment. We conclude that at high densities, increased intruder pressure from adult females had a greater impact on juvenile recruitment than did food abundance. Thus, our results suggest that patterns of space use, reproductive rates, and juvenile recruitment were more consistent with the pup-defense than the food-defense hypothesis for female territoriality.

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Introduction

A widely accepted paradigm in mammalian behavioural ecology is that males defend females and females defend resources (Emlen and Oring 1977, Ims 1987a). That resource for which females compete usually is considered to be food (Emlen and Oring 1977, Ostfeld 1985, 1990). Wolff (1993) recently challenged the food-defense hypothesis for female territoriality and proposed that female mammals defend territories to protect their pups from infanticide by conspecific females. Wolff (1993) questioned why females should defend space during the

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season when food was most abundant and argued that territory size did not seem to be based on energy demands. Bondrup-Nielsen (1986) and Wolff (1993) predicted that if females were defending food resources, a reduction in food availability should result in an increase in territory size or a decrease in reproductive success. Conversely, a decrease in the rate of pup survival with increasing density of unrelated adult females would support the pup-defense hypothesis. Although theoretical arguments have been made in favor of both hypotheses (Ostfeld 1990, Wolff 1993), predictions of each hypothesis have not been tested. We tested predictions of the food-defense hypothesis (1) that territory size of female rodents would correlate inversely with food abundance and (2) that reproductive success will decrease if females are unable to expand their territories when food abundance decreases. Conversely, the pup-defense hypothesis predicts that territory size and reproductive success (1) correlate inversely with the density of unrelated adult females, and (2) are not adjusted to food abundance. We removed 70% of the habitat of gray-tailed voles *Microtus canicaudus* (Miller, 1897) and monitored population size, density of adult males and females, territory size for adult females, reproductive activity, and juvenile recruitment before and after habitat removal. Gray-tailed voles are a typical herbivorous *Microtus* occupying the grasslands of the Willamette Valley of western Oregon, USA. Breeding occurs from March through November with a breeding lull in late summer and mid-winter. Adult body size ranges from 30–50 g, mean litter size is 4.4, the mating system is polygynous or promiscuous, home ranges of males are twice as large as those of females, and juvenile dispersal is male-biased (Wolff *et al.* 1994).

Methods

Study site and habitat removal

The study was conducted at the Hyslop Agronomy Farm of Oregon State University, approximately 10 km north of Corvallis, Oregon, USA (Wolff *et al.* 1994, Edge *et al.* 1996). The experimental units consisted of eight 0.2-ha (45 × 45 m) enclosures planted with alfalfa. Each enclosure was constructed of galvanized sheet metal approximately 90 cm high and buried 90 cm deep to prevent escape of or entry by burrowing animals. A 1-m wide strip along the inside of the fence within each enclosure was kept bare to minimize use by small mammals. Each enclosure initially contained 1850 m² (43 × 43 m) of alfalfa habitat. Twelve voles (6 males and 6 females) from our laboratory colony were introduced into each of the 8 enclosures in April 1994. On July 22–27, 70% of the alfalfa in 4 randomly selected enclosures was mowed and raked to remove all food and cover in the cleared areas to create 4 habitat-removal enclosures. The remaining habitat was partitioned into 25 small fragments, each 5 m × 5 m (25 m²) and separated from each other by 4 m of bare ground (Fig. 1). Cleared areas were kept bare by weekly mowing and removal of all vegetation. Each habitat patch was approximately 1/2 the size of an average home range for a female ($\bar{x} = 56 \text{ m}^2$; Wolff *et al.* 1994). The habitat in the 4 remaining enclosures was unmanipulated and served as controls.

Trapping procedures

One hundred Sherman live traps were placed in a 10 × 10 array with 4.3-m trap intervals in control enclosures. In habitat-removal enclosures, 4 traps were placed in what would become each

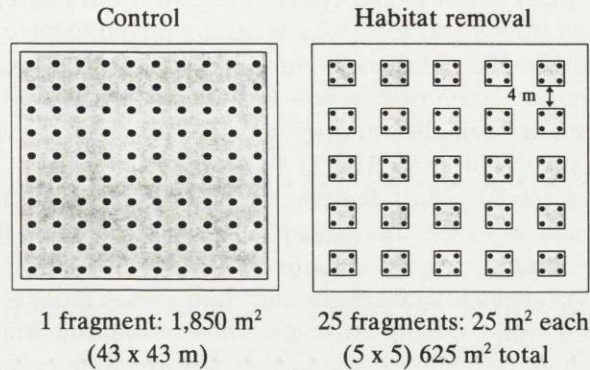


Fig. 1. Alfalfa distribution (shaded areas) and location of 100 traps in control and habitat-removal enclosures.

25-m² patch after habitat removal; each trap was placed 1 m in from the edge of the patch with 3 m between traps (total 100 traps; Fig. 1). Voles were trapped for 4 consecutive nights at 2-week intervals from May through early September 1994. Traps were baited with oats and sunflower seeds, set in the evening, and checked once a day at sunrise. All captured voles were ear-tagged for permanent identification and data on body mass, sex, reproductive condition, and trap location were recorded for each capture. Females were considered in reproductive condition if they were lactating, pregnant, or had widely parted pubic symphyses. Voles with body mass ≥ 30 g were considered adults.

Analyses

We used program CAPTURE (Rexstad and Burnham 1992) to estimate population size for each enclosure and trap period. Juvenile recruitment was measured by the number of recruits (newly tagged voles) captured in an enclosure per adult female captured in the same enclosure 4 weeks (2 trap periods) earlier. The time lag allowed recruits to reach trappable size. We examined recruitment in habitat-removal enclosures by calculating the number of recruits captured in each patch per pregnant female inhabiting the patch 4 weeks earlier.

Home-range sizes were estimated by the minimum-area-convex-polygon method for adult females caught 7–9 times during 4–6 weeks both before and after the date of habitat reduction. In the habitat-removal enclosures, only 3 or 4 voles met these criteria in 3 of the 4 enclosures, so home ranges were calculated for an additional 19 adult females that were caught 7–9 times after habitat removal but times prior to habitat removal. To increase sample sizes and demonstrate differences or similarities in home range sizes among cohorts and season, home ranges were calculated for an additional 27 adult females in control and 73 adult females in removal enclosures that were born during mid-summer and met the criteria of 7–9 captures as adults after habitat removal.

Results

Home ranges were calculated for 39 adult females in the 4 control enclosures and 23 adult females in the 4 habitat-removal enclosures prior to the time of habitat removal. After habitat removal, home ranges were calculated for the same 62 voles as before habitat removal, plus an additional 19 voles in habitat-removal

enclosures. Mean values for each parameter measured were determined for each enclosure and paired *t*-tests and ANOVA's were conducted using enclosures as the sample units ($n = 4$). We did not directly measure territorial defense, but 38 (62%) of the 62 home ranges estimated before habitat removal were exclusive with respect to other breeding females, and we considered the space voles occupied to be territories (see also Wolff *et al.* 1994).

Mean territory sizes for adult females were similar in control and habitat-removal enclosures prior to the time of habitat reduction ($F_{1,6} = 0.224$, $p = 0.653$; Fig. 2a). In both treatment categories, paired *t*-tests indicated that territory sizes after the date of habitat removal were smaller than those estimated before habitat removal (both $t_3 > 4.1$, $p < 0.026$). After the time of habitat removal, territories were significantly smaller in habitat-removal enclosures than in control enclosures ($F_{1,6} = 24$, $p = 0.003$; Fig. 2a). Mean territory sizes of females that were born in mid-summer and became adults in August were also smaller in removal ($\bar{x} = 16.0 \text{ m}^2$,

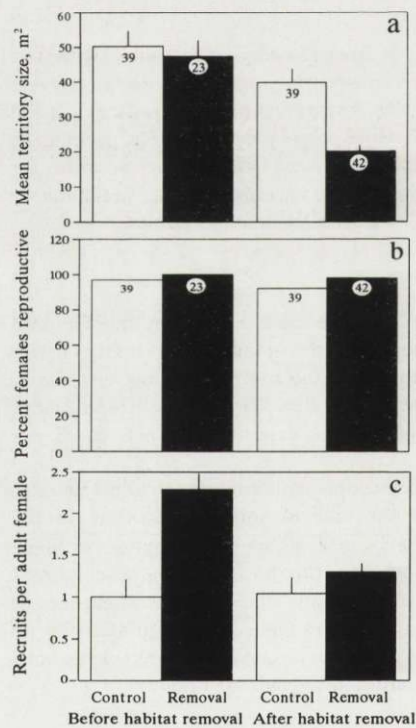


Fig. 2. Mean (\pm SE) territory sizes for adult female gray-tailed voles (a), percent of adult females in reproductive condition (b), and number of recruits per adult female (c) in control and habitat-removal enclosures before and after removal of alfalfa. Numbers on bars are sample sizes.

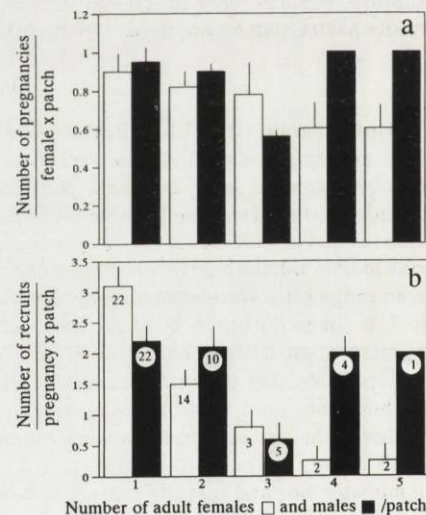


Fig. 3. The relationship between mean (\pm SE) number of pregnancies/female/patch (a), and number of recruits/pregnancy/patch (b), and the number adult females and adult males in a patch after habitat removal. For each sex adult in a patch, the number of individuals of the opposite sex in that patch ranged from 0 to 5. Numbers on bars refer to the number of females.

$n = 73$, $SE = 0.33$) than in control ($\bar{x} = 47.8 \text{ m}^2$, $n = 27$, $SE = 3.4$) enclosures ($F_{1,6} = 12.5$, $p = 0.012$). Females that had territories in cleared areas prior to habitat removal moved into the remaining patches. After treatment, only 8 (7%) of 115 adult females in habitat-removal enclosures had home ranges that extended beyond one 25-m^2 patch. Thus, after the time of habitat removal, territory sizes in habitat-removal enclosures were about 60% smaller than before treatment and 50% smaller than in controls.

Average population-size estimates prior to the time of habitat removal were 40 and 50 voles/enclosure (216 and 270 voles/ha of habitat) in control and habitat-removal enclosures, respectively (J. O. Wolff *et al.*, in prep.). After the time of habitat removal, peak population densities were 100 and 180 voles/enclosure (545 and 2 880 voles/ha of habitat) in control and habitat-removal enclosures, respectively. These numbers convert to ca 18.3 m^2 of exclusive habitat for each individual vole in control enclosures and only 3.5 m^2 in habitat-removal enclosures. As many as 9–12 adult and subadult voles occupied each 25-m^2 patch in 3 of the 4 habitat-removal enclosures. Thus, after the time of habitat removal, population densities had increased 2.5-fold in control enclosures and 10-fold in habitat-removal enclosures.

Reproductive rates remained comparable before and after treatment and between habitat-removal and control enclosures. The percentage of females in reproductive condition in control habitat prior to the time of habitat removal was 38 of 39 (96%) and after removal it was 36 of 39 (92%). The number of adult females in reproductive condition in habitat-removal enclosures prior to habitat removal was 23 of 23 (100%) and after removal it was 41 of 42 (98%). None of these differences was significant (all $\chi^2 < 1.05$, ns; Fig. 2b). For the females that were born in mid-summer, 89% (24 of 27) in control and 86% (63 of 73) in habitat-removal enclosures became reproductively active ($\chi^2 = 0.11$, ns).

Reproductive success could not be measured for individuals, but we attempted to measure mean juvenile recruitment per adult female per enclosure. Prior to habitat-removal, all 8 enclosures were presumed to be similar, however, recruitment rates were significantly higher in habitat-removal than in control enclosures before treatment ($F_{1,6} = 6.6$, $p = 0.043$). Recruitment rates were lower after treatment than before treatment in habitat-removal enclosures (paired $t_3 = 5.7$, $p = 0.011$), but did not differ significantly between control and habitat-removal enclosures after habitat removal ($F_{1,6} = 2.3$, $p = 0.18$; Fig. 2c). Thus, a 70% reduction in habitat did not adversely affect total juvenile recruitment rates compared to control habitat.

We examined pregnancy rates and juvenile recruitment rates with respect to number of adult females, males, and total density/patch in the habitat-removal enclosures. Because related females may behave nepotistically toward one another (Charnov and Finerty 1980, Ylönen *et al.* 1990, Lambin and Krebs 1991, Wolff 1995), we did not include in this analysis any females that were caught together at the same trap station as juveniles or as an adult and juvenile and thus could

have been closely related. For this analysis we used females that were born asynchronously and/or at least two trap stations away from each other and/or in different patches. After habitat removal, pregnancy rates did not differ significantly with the number of (presumably unrelated) females in a patch ($F_{3,41} = 0.43$, $p = 0.74$; Fig. 3a). However, the number of juvenile recruits/pregnancy/patch correlated inversely with the number of adult females/patch ($r = 0.47$, $F_{1,39} = 11$, $p = 0.002$; Fig. 3b). We observed no significant relationship between the number of adult males per patch and the number of pregnancies/female/patch ($r = 0.132$, $F_{1,41} = 0.713$, $p = 0.403$; Fig. 3a) or juvenile recruitment/pregnancy/patch ($r = 0.003$, $F_{1,41} < 0.001$, $p = 0.98$). Likewise, juvenile recruitment/pregnancy was not correlated with total density of adults/patch ($F_{1,40} = 0.030$, $p = 0.862$). Thus, recruitment rates were not affected by total density or density of adult males, but were adversely affected by the presence of unrelated adult females.

Discussion

Food is presumed to be a limiting resource for reproduction in female microtine rodents because of the animals' herbivorous diet, small size, and high energetic and nutritional demands for reproduction (Ostfeld 1985). If the function of territoriality among female rodents is to secure food that is both limited and necessary to successfully rear young, then manipulating the abundance of food should have predictable effects on the area that females occupy exclusively. Addition of food should result in smaller mean territory sizes, whereas reduction in food should result in larger territories. If females cannot defend larger areas, because their habitat is saturated with territorial females (Hestbeck 1982) or surrounded by barriers, then reproductive success should decrease, a prediction of the food-defense hypothesis not supported by our data.

We reduced the area of standing alfalfa by 70%, leaving patches half the size of a female's normal home range (Wolff *et al.* 1994) and produced population densities that approached 3 000 voles/ha. Instead of increasing or maintaining territory sizes, females generally confined their activities to 1 patch (or in some cases half a patch), apparently perceiving the 4 m between patches as a barrier. Despite being confined to 25-m² patches and sharing that space with up to 4 females and a total of 9–12 individuals, pregnancy rate was not diminished.

Reproductive activity of adult females did not change significantly over time. We did not measure plant biomass, but plant growth and above ground vegetation were reduced visibly from late July through August. The last rainfall was on June 16 and much of the vegetation was drying and turning brown by early to mid August. Thus, even with reduced quantity and apparent quality of food, vole reproduction and overall recruitment did not vary significantly even with a 60% reduction in territory size. These results suggest that females were occupying considerably larger space earlier in the year than was needed to meet the energy

demands of reproduction. The results also suggest that with densities approaching 3 000 voles/ha and up to 4 adult females and a total of 9–12 voles/25-m² patch, females were not able to maintain exclusive access to food or space.

Predictions of the food-defense hypothesis are supported only partially by previous studies. Reduction in territory size after food addition is well-documented in the small-mammal literature (eg Ims 1987b, Ostfeld 1986, Ylönen *et al.* 1988), and has been used as an argument for the food-defense hypothesis (Ostfeld 1990). In a review of food-supplementation studies, Boutin (1990) found that food supplementation often resulted in 2- to 3-fold increases in density and smaller home ranges. In these and other studies (eg Jones 1990), the relative contributions of additional food and increased intruder pressure to reduction in territory size could not be discerned. However, Desy *et al.* (1990) determined experimentally that home-range sizes of prairie voles *Microtus ochrogaster* were affected directly by population density and indirectly by food supplementation. This conclusion was supported by the experiment of Ostfeld and Canham (1995), who observed that home ranges of meadow voles *M. pennsylvanicus* decreased with increasing density, even though food availability decreased. Ostfeld and Canham (1995) however, did not mention if reproductive activity or juvenile recruitment were affected by reduced territory size. Boutin (1990) and Wolff (1993) proposed that a better test of the role of food in determining territory size would be a food-removal study, such as this experiment.

Our study did not directly test the pup-defense hypothesis for female territoriality, but were supportive of it. In that infanticide is hypothesized to be a mechanism for resource competition among females (Hrady 1979, Sherman 1981, Brooks 1984, Wolff and Cicirello 1991), we should expect an inverse relationship between juvenile recruitment and intruder pressure from neighboring unrelated females, but not from familiar males (ie probable fathers; Wolff 1995). Our results suggest this was the case. Pregnancy rates did not differ with territory size or when space was shared with as many as 4 other adult females or males, suggesting that food resources were adequate for conception and gestation. However, juvenile recruitment per pregnancy correlated inversely with the number of unrelated adult females sharing a 25-m² patch, but not with the number of adult males or total density. In this study we had 6 cases in which all adult females in a patch were presumably related (they were caught together in a trap earlier when pups were just being weaned). In these 6 cases, juvenile recruitment averaged 2.0 recruits/pregnancy with 2–4 related adult females/patch (J. O. Wolff and E. M. Schaubert, unpubl.). This result also suggests neither total density nor density of related females affect recruitment, but rather recruitment was affected only by density of unrelated females.

We do not know that infanticide was the mechanism for reduced recruitment, but our results are consistent with that assertion. An alternative explanation for the lack of juveniles in patches containing large numbers of females is that juveniles could have dispersed from the natal patch before they were first captured.

This seems unlikely, however, because dispersal rates of juveniles after treatment were very low in both treatment and controls (6–22%; J. O. Wolff *et al.*, in prep.). Also, because surrounding patches would contain unrelated individuals, juveniles would have to immigrate into high density patches of unrelated residents, which seems unlikely. Thus, it seems probable that if juveniles had entered the population, we would have captured them on their natal territories (or patches).

We conclude that at low densities, females occupied home ranges that provided much more food than was needed to meet their energy demands for reproduction. As densities increased, intruder pressure forced females into smaller space and the space occupied was not related to food abundance. Instead, our results suggest that scattered food is not a defensible resource for gray-tailed voles, nor probably for microtine rodents in general (Ostfeld 1985, 1990, Wolff 1993). We do not have a direct measure of infanticide, but the observation that juvenile recruitment, but not pregnancy rate, correlated inversely with density of unrelated females, but not males or perhaps related adult females suggests that reduced recruitment was associated with pup mortality and not overall reproductive condition of females. Thus, our results are more supportive of a pup-defense than a food-defense hypothesis for explaining space use by female gray-tailed voles. We contend that females ultimately defend their burrow, nest site, and pups and that any space larger than that area provides a buffer zone to keep intruders away from the nesting area. Intruder pressure at high densities reduces this size to a minimum and increases the potential for infanticide and pup mortality. Further research on the relative costs and benefits of territorial defense and intruder pressure will provide insight to the proximate causation and ultimate benefits of territoriality among female mammals.

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