

Gray-tailed voles prefer interior to edge habitats

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Abstract: We examined habitat preference of the gray-tailed vole (*Microtus canicaudus*), in an experimental fragmented landscape to test the hypothesis that female voles prefer interior to edge habitats. One hundred percent and 76% of adult female home ranges were located in interior habitat at low and high densities, respectively. The proportion of captures of females in edge habitat was lower at both low and high densities, but this difference was most pronounced at low densities. After selective removal of some females from interior and edge habitats at high densities, 8 (62%) of 13 females shifted their home ranges from edge to interior habitats compared to only 3 (15%) of 20 females moving from interior to edge habitats. Reproductive rates, survival, and body mass were comparable for females in edge and interior habitats. However, home range sizes were smaller for females in edge than interior habitats. These results support descriptive studies on some other small rodents e. g., *Clethrionomys* sp. and some *Microtus* sp., but differ from those of meadow voles, *M. pennsylvanicus*. We conclude that gray-tailed voles prefer interior to edge habitats and that the ratio of edge to interior habitats can potentially affect habitat selection and perhaps overall demography in fragmented landscapes.

Key words: Edge effects; Gray-tailed voles (*Microtus canicaudus*); Habitat patches; Home range; Landscape ecology

犬尾田鼠在斑块生境中更喜好内部区域

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摘要: 我们在斑块化的景观中实验测定了犬尾田鼠 (*Microtus canicaudus*) 的生境喜好, 验证下列假说: 在一斑块生境中, 与边缘区域相比, 雌性田鼠喜好内部区域。在低密度和高密度时成年雌性的巢区在生境内部区域分别占 100% 和 76%。高密度时在边缘区域雌性的捕获率较低, 这种差异在低密度时更突出。在高密度时通过选择性去除生境内部和边缘区域的一些雌体, 边缘区域 13 只雌体中 8 只 (占 62%) 的巢区发生从边缘到内部区域的转移, 内部区域 20 只雌体中只有 3 只 (占 15%) 的巢区向边缘区域转移。动物的繁殖率、生存和体重在两个区域之间没有差异。但是, 边缘区域个体的巢区比内部区域的要小。这些结果支持一些关于其他啮齿动物的研究观察结果 (如鼯类和田鼠类), 但与草原田鼠不同。因此在一斑块生境中, 与边缘区域相比, 长尾田鼠更喜好内部区域, 边缘区域与内部区域的比率可潜在影响动物的生境选择, 也可能会影响斑块化生境中的种群统计学特征。

关键词: 边缘效应; 犬尾田鼠; 生境斑块; 巢区; 景观生态学

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Fragmentation of continuous habitats results in loss of habitat and an increase in the proportion of edge to interior habitat. Numerous theoretical and empirical studies have addressed the consequences of habitat fragmentation to persistence of animal populations (e. g., Wiens *et al.*, 1993; Andrén, 1994; Diffendorfer *et al.*, 1995; Wolff *et al.*, 1997; and see Lidicker, 1999 for a review), but few studies have addressed the relevance of interior and edge habitat to habitat selection or individual fitness for mammals. Edges can be

defined as discontinuities in habitat features as perceived by focal individuals or species, and that in turn affect their performance in some biologically meaningful way (Bierregard *et al.*, 1992; Lidicker and Peterson, 1999). Habitat edges are created by habitat fragmentation, which creates heterogeneity in habitat quality (Williams-Linera, 1990; Lidicker and Koenig, 1996) and may have positive, negative, or neutral effects (Laurance, 1991; Saunders *et al.*, 1991; Lidicker and Peterson, 1999; Tattersall *et al.*, 2002). Fact-

ors that have negative effects may include poorer resources or increased exposure to predators (Murcia, 1995) and limitations to dispersal (Wolff and Davis-Born, 1997); positive benefit of edges may include reduce competition (Stamps *et al.*, 1987; Harper *et al.*, 1993) or higher quality food (Bowers *et al.*, 1996; Bowers and Dooley, 1999). Most studies that examined response of small rodents to edge and interior habitats have been descriptive and have shown that animals were more commonly observed in interior than edge habitats (e.g., Hansson, 1994; Mills, 1995; Lidicker and Peterson, 1999). However, Bowers and Dooley (1999) found that female meadow voles, *Microtus pennsylvanicus*, on edges had larger body sizes, longer residence times, higher reproductive rates, and larger home ranges than females in interior habitat. Bowers and Dooley (1999) and Bowers *et al.* (1996) concluded that females on edges were dominant to females in interior habitat and selectively preferred edge habitats. Similar results were found for meadow voles in a prairie ecosystem in Canada (Paischniak and Messier, 1998). In contrast, larger and older female gray-tailed voles, *M. canicaudus*, in alfalfa habitat were caught more often in interior than edge habitat (Peterson, 1996; Lidicker and Peterson, 1999). All previous studies on use of edge and interior habitat were descriptive and did not involve experimental testing of habitat preferences or responses to changes in density. We examined use of habitat by reproductively active adult female voles at low density, high density, and following selective removal of competitive neighbors to determine if remaining voles moved toward or away from edge habitat. The objectives of our study were to determine if reproducing adult, female gray-tailed voles preferred edge to interior habitat and if females living along edge habitat differed qualitatively from females living in interior habitat with respect to body mass, survival, home range size, or reproductive condition. We concentrated our study on females in that they are the resource-defending sex and use of space by males and juveniles is a function of location of females (Wolff, 1985; Ims, 1988; Bond and Wolff, 1999).

1 Materials and Methods

The study was conducted at the Hyslop Field Laboratory of Oregon State University located approximately 10 km north of Corvallis, Oregon, USA (Wolff *et al.*, 1994; Edge *et al.*, 1996). The experimental units consisted of four 0.2 ha (45 m × 45 m) enclosures planted with a mixture of pasture and old-field grasses. Each enclosure was constructed of galvanized

sheet metal extending approximately 90 cm above ground and buried 90 cm deep to prevent escape or entry by burrowing animals. A 1 m wide strip along the inside of the fence within each enclosure was mowed to bare ground and delineated the edge of a patch. Thus edge habitat was adjacent to bare ground. To monitor habitat use by voles, 81 Sherman live traps were placed in a 9 × 9 array with 5 m trap spacing in each enclosure. Trap rows were placed 1, 6, 11, 16, and 21 m from the edge of the patch. Traps located 1 m from the edge were considered edge traps, all others were considered interior habitat. The number of traps at each distance was 1-m (32 traps), 6-m (24), 11-m (16), 16-m (8), and 21-m (1). The amount of habitat space available around each trap was the same for all trap locations, thus expected capture rates would be the same for all trap distances. The 1-m mowed strip along the patch edge was used by voles to some extent (Wolff *et al.*, 1996) and was included in the assumed potentially inhabited area. We initiated the experiment on 12 May 1997 by introducing six adult males and six adult females into each enclosure. Voles were allowed to breed and increase in numbers until 12 September 1997. On 12 September, we reduced the population size to 8 females/patch by selectively removing some animals. We wanted to determine if animals would move to edge or interior habitat when densities were lowered to reduce competition and provide adequate space for movement. We then monitored the four populations until 20 December 1997.

Voles were live-trapped for 4 consecutive days at 2-week intervals from late May through 20 December 1997. Traps were baited with oats and sunflower seeds, set, and checked once a day. All captured voles were eartagged for permanent identification and data on body weight, sex, reproductive condition, and trap location were recorded for each capture. Females were considered in reproductive condition if they were lactating or pregnant. Animals were considered edge animals if >50% of their captures were in edge traps, all others were considered interior animals. Our study was conducted in three parts, low density, high density, and reduced density. The low density period was 6 wks from 19 May to 30 June when population size was 5–6 females in an enclosure. The high density period was 6 wks from 4 August to 12 September when population size was 12–19 adult females/patch (total of 50–70 voles/enclosure; 250–350 voles/ha). The experimental removal period (reduced density) was 22 September to 20 December when 8 females were in each enclosure. The numbers of males and juveniles in all patches were similar (Bond and Wolff, 1999) and should not have affected the results.

Homerange sizes were estimated by the minimum-area-convex-polygon method (Jenrich and Turner, 1969) using 7 – 9 captures/individual. The expected random proportion of captures in traps located at different distances from the edge based on number of traps at each distance were 1 m (40%), 6 m (30%), 11 m (20%), and 16 m (10%). Capture data were not used for the 21 m distance because only one trap station was located at this distance. The vegetation height and density were relatively uniform and similar at all distances from the edge in all four patches (Wang *et al.*, 1999). At low densities, females have exclusive home ranges with no to minimal overlap in use of trap stations (Wolff *et al.*, 1994) so we presumed all traps had an equal probability of capturing a vole. Data were analyzed using SAS version 6.0 and SYSTAT 6.0 for Windows. Data are presented as means (\pm one standard deviation) unless otherwise indicated.

2 Results

During the 6-week low density period, 23 females from the four patches, all of which had their home ranges in interior habitat, were caught a mean of 9.7 (\pm 3.03) times each. The most captures for any one female along edge habitat was 6 (37%) of 16. A mean of 8.8 (17%) of 50.3 captures/patch was in edge habitat which is lower than the expected 20 (40%) based on the proportion of traps in the interior and edge habitats (Table 1). The numbers of captures differed significantly among the four distances for two of the four patches and approached significance for a third patch (Table 1). The percent of captures was significantly lower than expected at the 1-m (edge) distance and higher than expected at all three interior distances (Fig. 1). All 23 females were pregnant at least once, and 22 (95%) of 23 females survived until the end of the 6-week period.

Table 1 Observed and (expected) number of captures of female voles at four distances from the edge at low density and high density in four 0.2 ha patches of grassland habitat. Captures in the interior trap, 21 m from the edge, are not included. N equals number of females present.

| Grid | N | Distance from edge, m | | | | Total captures | χ^2 | P |
|--------------|------|-----------------------|-------------|-------------|-----------|----------------|----------|-------|
| | | 1 m | 6 m | 11 m | 16 m | | | |
| Low density | | | | | | | | |
| 1 | 6 | 11 (21) | 13 (16) | 23 (10) | 4 (5) | 51 | 8.66 | 0.034 |
| 2 | 6 | 5 (13) | 13 (10) | 7 (6) | 5 (3) | 30 | 4.46 | 0.216 |
| 3 | 5 | 14 (26) | 32 (20) | 12 (13) | 5 (7) | 63 | 6.68 | 0.083 |
| 4 | 6 | 5 (23) | 24 (17) | 15 (12) | 13 (6) | 57 | 22.53 | 0.001 |
| Total | 23 | 35 (80) | 82 (60) | 57 (40) | 27 (20) | 201 | 25.04 | 0.001 |
| Mean | 5.8 | 8.8 (20) | 20.5 (15) | 14.3 (10) | 6.8 (5) | 50.3 | 6.16 | 0.104 |
| High density | | | | | | | | |
| 1 | 21 | 51 (56) | 47 (42) | 25 (28) | 11 (14) | 134 | 0.91 | 0.822 |
| 2 | 13 | 16 (34) | 42 (26) | 12 (17) | 14 (9) | 84 | 12.17 | 0.007 |
| 3 | 19 | 46 (50) | 42 (38) | 28 (25) | 9 (13) | 125 | 1.26 | 0.739 |
| 4 | 15 | 25 (36) | 43 (27) | 8 (18) | 10 (9) | 86 | 9.45 | 0.024 |
| Total | 68 | 138 (172) | 174 (129) | 73 (86) | 44 (43) | 429 | 11.485 | 0.009 |
| Mean | 17.0 | 34.5 (43.0) | 43.5 (32.3) | 18.3 (21.5) | 11 (10.8) | 107.3 | 3.115 | 0.374 |

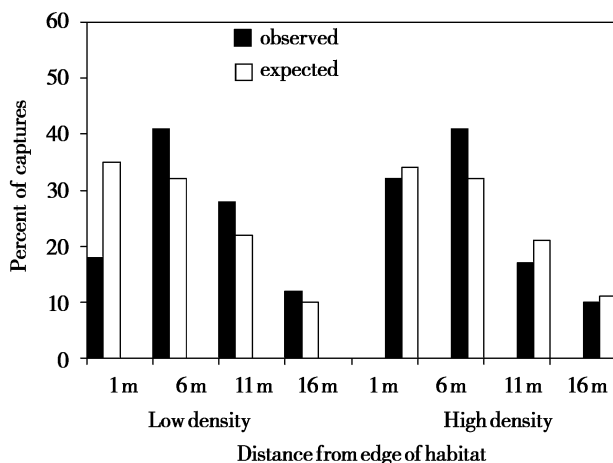


Fig. 1 Percent of captures at various distances from edge habitat at low and high densities for gray-tailed voles in four 0.2 ha patches of grassland habitat

During the 6-week high density period, 68 females were caught a mean of 6.5 (\pm 0.41) times each. Of

these females, 52 had home ranges in interior habitat and 16 in edge habitat. Overall, fewer animals than expected were caught in edge than interior traps based on the number of traps available; however these differences were significant for only two of the four patches (Table 1). In all four enclosures and overall, a greater number of captures occurred at the 6-m distance than in the edge or more interior patches (Table 1 and Fig. 1). No differences occurred between females in interior and edge habitats with respect to body weight, reproductive rate, or survival (Table 2). Females, however, had smaller home ranges in edge than interior habitats (Table 2).

For the reduced density experiment, we selectively removed some females from edge and interior portions of habitat in four patches such that we had 7 – 9 females relatively evenly spaced remaining in each enclosure. In the four enclosures, 13 remaining females had home

ranges in edge habitat compared to 20 in interior habitat. During the next 6 wks, 8 (62%) of the 13 females moved from edge to interior habitat compared to only 3 (15%) of 20 females moving from interior to edge habitat ($\chi^2 = 7.83$, $P < 0.01$). For females that moved from edge to interior habitat after the removal period, the mean number of captures/female in edge habitat decreased from 3.3 (± 1.1) to 0.9 (± 1.0) and in interior habitat increased from 2.2 (± 1.2) to

4.4 (± 2.1). For females that moved from interior to edge habitat, the mean number of captures/female in edge habitat increased from 2.0 (± 0.8) to 3.3 (± 2.1) and in interior habitat decreased from 3.3 (± 1.9) to 1.9 (± 1.3). Some females moved their entire home range, whereas others just shifted their activity. By the end of the experiment, only 7 of 33 females in the four patches had >50% of their captures in edge habitat.

Table 2 Characteristics of female gray-tailed voles with respect to home ranges in interior and edge habitats at high density in four 0.2 ha patches of grassland habitat

| | Interior | Edge | Stat | P |
|---------------------------------|---------------------|---------------------|-------------------|-------|
| Home range size, m ² | 29.0 (± 4.87) | 16.5 (± 7.13) | $F_{1,6} = 8.493$ | 0.027 |
| Body weight, g | 44.5 (± 3.52) | 43.6 (± 3.00) | $F_{1,6} = 0.169$ | 0.695 |
| Percent reproductive | 94% (49/52) | 93% (13/14) | $\chi^2 = 0.001$ | 0.973 |
| Percent survival | 81 (41/51) | 87 (13/15) | $F_{1,6} = 0.017$ | 0.901 |

3 Discussion

Our experimental results support previous observational studies that some small rodents avoid edge habitats (e.g., field voles, *Microtus agrestis*, and bank voles, *Clethrionomys glareolus*, Hansson, 1994; and California red-backed voles, *Clethrionomys californicus*, Mills, 1995). In our study, at low densities, 100% of female gray-tailed voles had their home ranges in interior habitat. At the lower densities, females maintained relatively exclusive home ranges with minimal to no overlap with other adult females. As populations increased in size, some females began occupying edge habitat, but in no patch at any time were more females found in edge than interior habitat. The more even distribution of animals in edge and interior habitats at high density was likely due to territorial behavior and habitat saturation forcing individuals to edge habitat. However, even at the higher densities, females tended to avoid the extreme edge. The higher number of captures at the 6-m distance may have been due to competitive pressure from females in the center of a patch and an avoidance of edge habitat. This distribution of animals along edge habitat fits the predictive model of Lidicker (1999; Fig. 2). Females on the edge had smaller home ranges than females in interior habitat that may have resulted from pressure of more dominant females in interior habitat and an avoidance of the edge squeezing them into a narrow 5-m band of habitat.

After removal of some females from edge and interior habitat created vacant space in both areas, 62% of females in edge habitat moved to interior habitats compared to only 15% of females in interior habitat moving to edge habitat. In some cases, females abandoned their previous home ranges, but in most cases females

simply shifted their use of space within an established home range. Females in general seemed to avoid use of edge habitats at all densities, but this was most obvious at the lower densities. By the end of the removal experiment, 79% of the females in the four patches were avoiding edge habitat. Our results support the study of Peterson (1996) and Lidicker and Peterson (1999) who found that gray-tailed voles in alfalfa habitats also were caught more frequently in interior than edge habitats.

Our results differ from those of Bowers *et al.* (1996) and Bowers and Dooley (1999) who concluded that female meadow voles did better on edge than interior habitats. Bowers *et al.* (1996) found that females in edge habitat had larger and more exclusive home ranges, larger body sizes, longer residence time, and higher reproductive rates than females in interior habitat. In our study, female voles occupied edge habitat only at high, but not at low densities. These voles, however, were not qualitatively different from females that remained in interior habitats. Body size, reproductive rates, and survival were comparable for females in both habitat areas. Bowers *et al.* (1996) were not able to determine the benefits of living in edge habitat, but suggested that food may have been of higher quality than in interior habitats. On the other hand, predation may be higher along edge than in interior habitats, and voles in general seem to seek higher cover when it is available (Baker and Brooks, 1982; Desy and Batzli, 1989; Wolff and Davis-Born, 1997).

We were not able to demonstrate an adaptive advantage for voles living in interior compared to edge habitat, but predation risk could be a factor. We were not able to measure predation during our study, but during winter, raptor predation is intensive in our study

area and American kestrels, *Falco sparverius*, and northern harriers, *Circus cyaneus*, hunt for voles extensively in our patches and in surrounding areas (Wolff *et al.*, 1999). The time spent foraging by raptors and capture success are greater in the open habitats than in areas with considerable cover (Wolff *et al.*, 1999). In a separate study in which we mowed half of the patches and left the other half unmowed, voles moved from the mowed area into the center of the tall grass habitat (Wolff and Davis-Born, 1997). Predation risk seems to be a major factor affecting habitat use by voles in our area.

We conclude that interior habitat is preferred to edge habitat in gray-tailed voles and perhaps for many other small mammal species (e.g., Hansson, 1994; Mills, 1995; Murcia, 1995) and more likely for habitat specialists than generalists (Bock *et al.*, 2002; Tattersall *et al.*, 2002). Fragmented habitats increase the ratio of edge to interior habitat which should in turn affect demography of voles in altered landscapes (Barrett and Peles, 1999; Delattre *et al.*, 1999). Our study was conducted with a hard edge in which no cover, food, or competitors occurred in adjacent habitat; however this habitat is common in agricultural settings where much of the habitat is under cultivation. Further experimental studies on the response of small mammals and other mammalian species to edge and interior habitats are needed to determine the selective advantages and disadvantages of microhabitat selection at this scale and how they relate to different life histories (sensu Lidicker 1999; Tattersall *et al.*, 2002). Further studies that attempt to demonstrate the interrelationships among intraspecific competition, habitat quality in interior and along edge habitats, and vulnerability of animals to predation pressure are needed to develop a more comprehensive theory of how animal species respond to fragmented habitats.

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