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Old Growth Mngt

How red-backed voles find habitat patches

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Abstract: The purpose of this study was to discover how red-backed voles (*Clethrionomys gapperi pallescens*) found preferred habitat patches. Two hypotheses tested were that voles discover habitat patches by chance, and that they perceive them from a distance and travel towards them. The distance at which voles detected a wooded habitat was determined by measuring the accuracy of orientation at different distances. Animals were released in an unfamiliar grassland at one of five distances (0–20 m) from the boundary of an adjacent unfamiliar woodland and tracked using the spool and line technique. At all distances, the voles oriented towards the woods. However, their reaction was much weaker at greater distances. Thus, reaction to the woodland was not an "all or nothing response"; the closer the voles came to the woods, the straighter were their paths and the more directly they oriented towards the woods. This adds to our understanding of how habitat fragmentation affects voles. A between-patch distance of 20 m does not completely isolate red-backed voles, but a distance equivalent to a home-range diameter (60–70 m) likely would.

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Résumé : Nous avons tenté de déterminer de quelle façon les Campagnols à dos roux de Gapper (*Clethrionomys gapperi pallescens*) trouvent des îlots de leur habitat préféré. Deux hypothèses ont été vérifiées : les campagnols découvrent ces îlots par hasard, ou alors ils les perçoivent à distance et s'y rendent. La distance de repérage d'un habitat boisé a été évaluée en mesurant la précision de l'orientation à diverses distances. Des campagnols ont été relâchés dans une prairie à laquelle ils n'avaient jamais été exposés, à l'une de cinq distances (0–20 m) de la bordure d'un boisé adjacent et ils ont été suivis au moyen d'un fil attaché. Les campagnols se sont orientés vers le boisé quelle qu'ait été la distance de leur point de départ. Cependant, la réaction s'est avérée plus faible aux distances les plus éloignées. La réaction des animaux n'en était donc pas une du « tout ou rien » : plus ils approchaient du boisé, plus leur itinéraire était rectiligne et plus ils s'orientaient directement vers le bois. Ces observations nous permettent de mieux comprendre comment la fragmentation de l'habitat affecte les campagnols. Une distance de 20 m entre deux îlots de leur habitat préféré n'isole pas complètement les campagnols, mais une distance égale au diamètre de leur domaine vital (60–70 m) les isolerait probablement.
[Traduit par la Rédaction]

Introduction

Habitat selection is typically measured by determining that animals use one habitat more than others (e.g., Etheredge et al. 1989; Barnum et al. 1992; Kremsater and Bunnell 1992; Samuel and Kenow 1992; Aebischer et al. 1993; Barbour and Litvaitis 1993). Most studies have concentrated on *which* habitats are selected, but we also need to know the mechanism of selection. Animals can select habitats in two non-mutually exclusive ways: they enter them more often (Kramer and Weary 1991) or, once there, stay longer in them (Charnov 1976; Pyke 1984).

Understanding these selection mechanisms might help in understanding how animals respond to habitat fragmentation. For example, red-backed voles (*Clethrionomys gapperi pallescens* Vigors) prefer wooded habitats (Clough 1964; Krebs and Wingate 1976; Morris 1983), and their numbers drop significantly following clear-cutting (Martell and Radvanyi 1977). It has been suggested that they die, rather than emigrate (Martell 1983), so perhaps the clearcuts are too large for voles to find the wooded habitats at the edge. Thus, understanding how and from what distance animals find preferred habitats might allow us to predict optimal habitat patch sizes.

Purpose

Our objectives were to find out how red-backed voles found preferred habitats (wooded areas). Two hypotheses were (1) that voles discover the woodland by chance, and once the woods are encountered they remain there, and (2) that voles perceive the woods from a distance and travel towards them.

Methods

We released voles in grassland at various distances from a wooded area and tracked their paths for the first 50 m traveled. Small mammals readily learn habitat features within their area of daily movement (Alyan and Jander 1994; Jamon 1994). To ensure that we were testing for habitat detection rather than location-based navigation, we tested the voles more than 1 km from their point of capture (Jamon and Benhamou 1989). Our general procedure was similar to that of Zollner and Lima (1997).

The experimental area was located at McElmons Pond near Debert, Nova Scotia, Canada. The area consisted of a grassy meadow adjacent to a woodland, with a sharp boundary between the two habitats. The meadow was ~2 ha in size with a grass height of 10–30 cm, with little dead grass cover. The wooded area contained approximately 10% deciduous tree cover (*Acer rubrum* L. (red maple, ~6–10 m tall), *Betula populifolia* Marsh. (gray birch), and

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Table 1. Proportions of thread inside versus outside the woodland habitat for voles which entered the woods, showing that voles selected woodland habitat.

Release location	n	Proportion in woodland	Proportion in grassland	Test of significance
0 m	4	1.00	0.00	Exact binomial, $p = 0.0623$
All other distances[a]	14	0.96±0.05	0.04±0.05	$t = 2.29$, $p = 0.025$

Note: n is the number of voles that entered the woods.

[a] Measurements were taken once voles had crossed the boundary between the two habitats. Values are given as the mean ± 95% confidence limits.

Table 2. Orientation of voles at various distances from the woodland.

Distance from boundary (m)	n	Orientation (deg.)[a]	V	p
5	15	6.7±8.2	0.953	<0.0001
10	12	0.4±19.4	0.821	<0.0001
15	7	14.3±46.6	0.384	<0.10
20	6	32.3±47.8	0.386	<0.10

Note: n is the number of voles which crossed at that distance. Each vole could be counted only once at each distance. V is a measure of nonrandom movement towards 0° (the woods).

[a] Mean ± 95% CI.

Prunus virginiana L. (chokecherry)), 90% shrub cover (predominantly *Alnus* spp., ~3–4 m tall), and 60–80% herbs. Both the wooded and grassland habitat were capable of supporting red-backed voles (Iverson and Turner 1972).

Voles were livetrapped using Ugglan multiple-capture traps. The animals were driven to the release area with covers on the traps so that they could not see their surroundings. We attached a 0.5-g spool of thread (~55 m long) encased in heat-shrink plastic to the back of each animal (Boonstra and Craine 1986). Traps were placed parallel to the boundary between the habitat types, with a randomly assigned exit direction to prevent any bias towards a particular initial travel direction. At the release site, the trap was opened to allow the vole to exit by choice. After a minimum of 2 h (to ensure that voles were not influenced by human activity) the thread trail was followed.

Animals were released in the grassland 0, 5, 10, 15, or 20 m from the grassland/woodland boundary in each of five release rows. The release rows were situated 9 m apart and perpendicular to the boundary. To minimize the effects of odor of previously released voles, release rows were blocked against time in a latin square design. Twenty voles (4 individuals at each distance), 17 males and 3 nonlactating females, ranging in mass from 13 to 24 g were released at the experimental area between 14 June and 2 October 1993.

To measure habitat selection, the proportions of thread inside the woodland and grassland habitats were calculated and compared for those voles released at the boundary (0 m) and for all other voles once they crossed the grassland/woodland boundary. Proportions were normalized with an arcsine transformation (Krebs 1989).

The orientation of each vole was measured at each test distance. Orientation was the direction of the path over a net distance of 5 m, with 0° pointing straight to the woodland. Mean angle and angular deviation were estimated using circular statistics (Batschelet 1981), and a V test was performed to determine if the voles at each distance were oriented randomly or significantly more towards the woods.

Tortuosity (gross distance/net distance traveled) was used as a measure of path "crookedness" and was determined for each animal over a net distance of 5 m at each test distance. Overall tortuosity in the grassland was measured directly and overall woodland tortuosity was calculated from the maps. A pooled t test could not be used to compare the two mean tortuosity values because of extreme nonnormality, therefore a χ^2 test was used to test for interaction between tortuosity and habitat.

Tortuosity measurements were dependent among distances, since each animal yielded several measurements (one at each distance). To test for a general relationship between tortuosity and distance, we first estimated the correlation between tortuosity and distance for each animal. These estimates were now independent among animals, so we used a t test to test for an overall non-zero correlation.

All of these path statistics were measured at each test distance for each vole. However, since some voles did not reach the wooded area, sample sizes (the number of individual voles crossing at a particular distance) varied among test distances. All means are given ± 95% confidence limits.

Results

Voles' paths were significantly straighter in the grassland (path tortuosity 1.3 ± 0.2) than in the wooded area (26.8 ± 32.7; comparison of the numbers of tracks that were straighter in wooded versus grassland area: binomial test, $p < 0.0001$). Once voles reached the boundary between the grassland and woodland, they traveled significantly farther inside the woodland habitat than back into the grassland (Table 1). This confirms that they selected the wooded area.

At distances <10 m, voles oriented themselves strongly and significantly towards the woods, while at greater distances (15–20 m) voles were less directed (Table 2). Furthermore, while the paths were oriented closer together and were straighter closer to the woodland (mean $r = 0.66$, $t = 3.85$, $n = 13$, $p < 0.003$), both changes were gradual (Figs. 1 and 2, respectively). This means that the voles' responses were not all or nothing.

Discussion

The results concerning both orientation and tortuosity support the hypothesis that the voles do not discover the woodland through the random, unoriented movement exhibited by some spiders (Gillepsie 1987), but rather by directed, oriented movement, indicating a perception of the woodland habitat. Zollner and Lima (1997) found similar results for white-footed mice. However, we cannot say how the voles know the woodland is there.

Vision may have played a role in the voles' detection of the

Fig. 1. Relationship between orientation deviation of vole paths in the grassland and distance from the grassland/woodland boundary. Orientation deviation measures how close vole paths were to each other at each distance. Fifteen, 12, 7, and 6 voles crossed at 5, 10, 15, and 20 m. respectively). Vole paths were closer, indicating that selection of the woodland habitat became stronger, closer to the boundary.

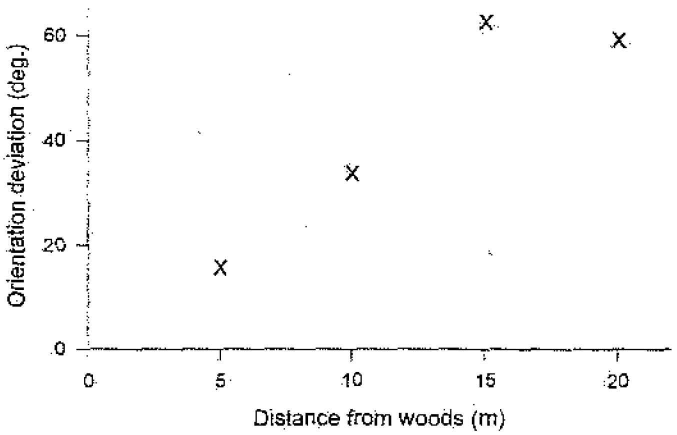
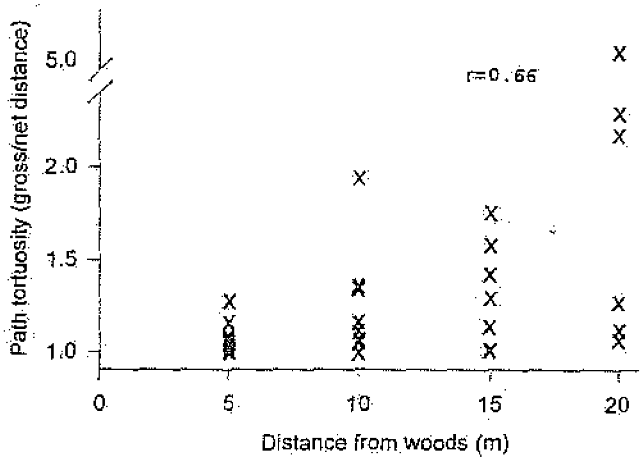


Fig. 2. Relationship between vole path tortuosity (crookedness; the grassland and distance from the grassland/woodland bound Fifteen, 12, 7, and 6 voles crossed at 5, 10, 15, and 20 m, respe tively. Vole paths were straighter, indicating that selection of th woodland became stronger, closer to the boundary (among anin mean $r = 0.66$; $t = 3.85$; $n = 13$, $p < 0.003$).



woods, as the grass was not high enough nor was there enough of a dead grass mat in the grassland to prevent them from seeing the woodland. Vision has been shown to be an important factor in the navigation of some other small mammals (Teroni et al. 1987), but is not necessarily the only sense used in navigation (Dashiell 1959). Other factors that may have aided the voles include odors, sounds, or shadows associated with the woods. All these cues would decrease in intensity with distance from the woods.

Why was the voles' response to the woodland gradual and not all or nothing? The reason could be that the voles gradually detected the woodland, or that, once it was detected, they gradually chose to go towards it. Our study cannot differentiate between the two; this question has generally not been addressed before and needs further study.

There are some ways to expand this preliminary study. First, use many experimental sites: we (after Zollner and Lima 1997) used only one experimental site and there is a chance that the animals cued into some unique feature of the site rather than wooded habitat in general. Second, test the effect of even greater distances. The voles showed a decreased response to the woods at 15–20 m, yet their orientation at that distance was not completely random. On the other hand, the increase in path tortuosity and orientation deviation at greater distances suggests that 20 m is at the edge of their response distance. White-footed mice detected forested areas from similarly short distances (Zollner and Lima 1997).

The results of this study add to our understanding of how habitat fragmentation affects voles. When distances between patches are small, animals readily cross the unfavorable habitat, treating the whole area as part of their home range (Rajskajurgiel 1992; Kozakiewicz et al. 1993). However, as distances between patches increase, the animals reach a point at which they no longer readily cross the unfavorable habitats. A between-patch distance of 20 m does not completely isolate red-backed voles, but it is likely that a slightly greater distance would. This is much less than the 60- to 70-m diameter of red-backed voles' home ranges. Since habitat selection based on directed movement, the area of grassland required create a true island would be larger than that required if t habitat was found by random movement. White-footed mi are similar in size to voles and their response distances similarly short. It would be interesting to know if detecti distance is mostly dependent on animal size.

Animals can respond to habitat on many different spati scales (Addicott et al. 1987; Kotliar and Wiens 1990). On large scale, habitat selection is studied as animal emigratio immigration, migration, and orientation (Orians 1991). Mec anisms used by animals to navigate and orient on a larg scale might also be used to find smaller scale habitat patche In this study, we have tried to bridge the gap between orient tion and the traditional concept of habitat selection, studyin orientation as part of the selection process.

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