

# An experimental test of habitat selection by rodents of Algonquin Park

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**Abstract:** Using an enclosure experiment, we tested whether substrate selection by deer mice (*Peromyscus maniculatus*), redback voles (*Clethrionomys gapperi*), and woodland jumping mice (*Napaeozapus insignis*) matched habitat-use patterns determined from trapping data. Mice were introduced into a 5 m diameter enclosure containing substrates from three habitats: maple, mixed, and coniferous forest. Trapping data were taken from a long-term monitoring study of small-mammal populations in Algonquin Park, Ontario. We used data from 1991–1995 from the three habitats used in the enclosure experiment. If competition or predation affects habitat distribution patterns, then, given a choice, mice should select different substrates in the enclosures from those they use in the field. Alternatively, if habitat use is not constrained by interactions with competitors or predators (i.e., if small mammals select habitats), then habitats used in the enclosure should match habitat distributions observed in the field. Habitats used in the field did not match habitats selected in the enclosure experiment for either deer mice or woodland jumping mice. Redback voles selected habitats similar to those used in the field. We conclude that interspecific competition and (or) predation may limit availability of habitats for deer mice and woodland jumping mice.

**Résumé :** Une expérience dans une enceinte nous a permis d'examiner si le choix du substrat chez la Souris sylvestre (*Peromyscus maniculatus*), le Campagnol à dos roux de Gapper (*Clethrionomys gapperi*) et la Souris sauteuse des bois (*Napaeozapus insignis*) correspond aux patterns d'utilisation de l'habitat déterminés lors de captures en nature. Les animaux ont été placés dans une enceinte de 5 m de diamètre contenant des substrats de trois habitats, l'érablière, la forêt mixte et la forêt de conifères. Les données sur les captures ont été empruntées à une étude à long terme des populations de petits mammifères dans le parc Algonquin, Ontario. Nous avons utilisé les données recueillies de 1991 à 1995 dans les trois mêmes habitats que ceux utilisés dans les expériences en enceinte. Si la compétition ou la prédation affectent les patterns de répartition des habitats, il faut s'attendre à ce que, devant un choix, les rongeurs choisissent dans les enceintes des substrats différents de ceux qu'ils utilisent en nature. Inversement, si l'utilisation de l'habitat n'est pas affectée par les compétiteurs ou les prédateurs (i.e., les petits mammifères choisissent leur habitat), on s'attendra à ce que les habitats choisis dans les enceintes correspondent à ceux utilisés en nature. Les milieux choisis en nature ne correspondaient pas à ceux choisis dans les enceintes, ni chez la Souris sylvestre, ni chez la Souris sauteuse des bois. Les Campagnols à dos roux de Gapper ont choisi les mêmes habitats en nature et dans les enceintes. Nous concluons que la compétition interspécifique et (ou) la prédation peuvent limiter la disponibilité des milieux chez la Souris sylvestre et chez la Souris sauteuse des bois.

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## Introduction

Habitat selection can be defined as the active choice of a habitat from a range of alternatives in the absence of constraints such as competition, predation, or parasitism (Partridge 1978). Habitat use may not reflect habitat selection because distributions among habitats may be the result of ecological constraints on habitat-selection patterns (Partridge 1978). "Habitat selection" and "habitat use" are often used interchangeably, the distinction rarely being made.

For small mammals, habitat selection is often inferred from habitat distributions based on trap captures (e.g.,

Dueser and Shugart 1978, 1979; Dueser and Hallet 1980; Hallet et al. 1983; Vickery et al. 1989), but various small-mammal species may be restricted to certain habitats by interspecific competition (Grant 1969, 1971, 1972; Redfield et al. 1977; Holbrook 1979; Boonstra and Hoyle 1986) or predation (Kotler et al. 1991; Dickman 1992; Hughes et al. 1994). In other words, habitats that could be selected are not necessarily available to be used. Habitat distributions may also be the result of past evolutionary events, such as "the ghost of competition past," which may predispose individuals to select certain habitats in response to past ecological conditions (Connell 1980; Abramsky and Sellah 1982; Davic 1985). A rigid, experimental approach would be most appropriate for determining the mechanisms behind habitat distributions.

Few studies have tested the independent effects of habitat preference and interspecific interactions on habitat selection by individual small mammals. An appropriate approach for distinguishing between habitat selection and use would involve determining habitat preference in the absence of competition and predation. In this way, habitats that are selected can be

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compared with those used in the wild, allowing the effect, if any, of competition or other factors to be determined.

The relative abundance of species among habitats can be used as a measure of habitat use (Rosenzweig 1989). To measure habitat use, we used long-term monitoring data from Algonquin Park, Ontario, Canada, which have shown that the abundance of deer mice (*Peromyscus maniculatus*), redback voles (*Clethrionomys gapperi*), and woodland jumping mice (*Napaeozapus insignis*) varies among habitats (Brooks et al. 1995). To measure habitat selection by these three species, we used enclosures containing substrates from three habitat types. Enclosure experiments can provide a transition between difficult field studies and unnatural laboratory environments (Hairston 1989).

Our objective was to determine whether evidence of habitat use matched habitat-selection patterns determined experimentally. If external processes such as competition or predation affect habitat distribution patterns, then, given a choice, individuals should select substrates in the enclosures that differ from those used in the field (Walker 1964). Alternatively, if species' habitat use is not constrained by interactions with competitors or predators (i.e., if small mammals select habitats), then substrates used in the enclosure should correspond to habitat distributions observed in the field.

## Methods

### Long-term trapping

The trapping data were part of a long-term small-mammal monitoring program at the Wildlife Research Area in Algonquin Park (45°30'N, 78°40'W) (Brooks et al. 1995). Three hardwood (maple, *Acer saccharum*), three mixed (spruce and aspen, *Picea glauca* and *Populus tremuloides*), and two coniferous (spruce and pine, *P. glauca*, *Pinus strobus*) forest transects were monitored and used in the analysis. These transects were monitored annually using standardized methodology (Blake and Falls).<sup>2</sup> Transects consisted of 10 pairs of Sherman live traps (23 × 9 × 7.5 cm) set at 10-m intervals. Traps were baited with sunflower seeds (soaked in water for 4–6 h) for 3 consecutive nights every 2 weeks for 20 weeks from mid-May to late September. Captured deer mice, eastern chipmunks (*Tamias striatus*), woodland jumping mice, and redback voles were sexed, aged, weighed, ear-tagged with Monel fingerling tags, and released at the point of capture. We used data from 1991–1995 to estimate levels of relative abundance in each of the three habitats.

The total number of captures per 100 trap-nights was used as an index of relative abundance. We grouped captures from all transects within each habitat for each year, therefore we had measures of relative abundance for the three habitats over 5 years. ANOVA and Tukey's multiple comparison test were conducted to determine which habitat type had the highest relative abundance within each species.

### Enclosure experiment

All experiments were conducted at the Wildlife Research Station. Ten adult (5 males, 5 females) redback voles, deer mice, and woodland jumping mice were captured using Sherman live traps at various sites throughout the Wildlife Research Area. Males had

enlarged testes and females were not noticeably pregnant or lactating. Experimental subjects were housed indoors for a maximum of 7 days in plastic cages (15 × 20 × 30 cm) and provided with nesting material, water, rat chow (Purina Laboratory rat diet No. 5001), and sunflower seeds ad libitum. Animals were individually marked with Monel fingerling ear tags.

Four enclosures were built in an open area of mixed forest. Each enclosure was circular (5 m diameter) and constructed from sheet metal (16 m long, 1 m wide) supported around the outside perimeter with stakes. The original substrate was removed from the enclosure and then sections of forest floor, including leaf litter, dead wood, shrubs, and 6–10 cm of soil, were transplanted from the forest habitats to the enclosures. The floor of the enclosure consisted of the same three habitat types monitored during the long-term trapping program, i.e., hardwood (maple), mixed (spruce–aspen), and coniferous (spruce–pine) forest, each being of equal area and arranged in a pie configuration. A tarpaulin with holes randomly cut in it was hung 1–1.5 m above the enclosure to simulate a patchy forest canopy.

Single animals were placed in the middle of the enclosure at 22:00–23:00 and left overnight (6–8 h). We randomized which species was being tested on any given night. We used each enclosure every second night to reduce the effects of odours and conducted trials only on dry nights. Although trapping occurred on wet and dry nights, comparisons between use and preference should still be possible, since Attuquayefio (1995) concluded that habitat use by small mammals in Algonquin Park was not affected by weather. All trials were conducted from June to August 1995.

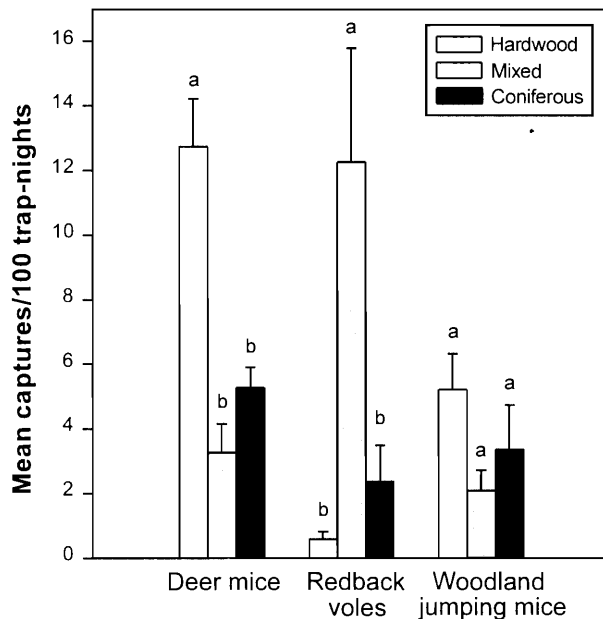
Movements of animals were tracked using the spool and thread technique (Boonstra and Craine 1986). Prior to attachment of the spool, animals were anaesthetized by placing them in a glass jar with an air tube and cotton soaked in methoxyflurine (Metofane, Janssen Pharmaceutica). Anaesthetic was used to prevent the rodents from becoming overly stressed during handling. Mice were kept in the jar until they stopped moving (approximately 10 min). They were then removed from the jar and the spool was attached to the upper back using a surgical adhesive (Vetbond, 3M) (Animal Care Protocol No. 95RO99, Animal Care Committee, University of Guelph). Animals were left in the cage until their behaviour appeared normal, typically 10 min (R.P. Strickland, D.V.M., personal communication).

The length of string deposited in each habitat type by the animal was measured. Habitat selection was assessed from arcsine-transformed values for the proportion of string in each habitat type. We assumed that the length of string in each habitat type was a reliable index of habitat use. We did not test this assumption, since verification would be fraught with difficulties. Direct nocturnal observations would have to be made, but there is no guarantee that the light and the presence of an observer would not affect the activity patterns of these rodents (V.O. Nams, personal communication). Habitats in the enclosure with large amounts of string were considered selected or preferred because competition and predation were absent. The use of a tracking technique is superior to the use of trapping data alone because it is not limited to one observation per individual each night, does not involve the introduction of supplementary food and shelter, which may attract trap-happy individuals, and ensures that activity is sampled in all habitats (Vickery 1981). Animals were recaptured, the spools removed, and the animals released at their original point of capture. Spools typically contained approximately 100 m of string, but during some trials the spool fell off before it was exhausted, so the total length of string laid down by each animal typically ranged between 70 and 100 m. Although we could not determine the period of time required for an individual animal to dispense the thread, based on our pilot observations we assumed that at least 2 h would be required.

To determine whether we could pool males and females of each

<sup>2</sup> S. Blake and J.B. Falls. 1987. Manual of field methods used for long-term small mammal trapping in Algonquin Park. Unpublished manuscript, University of Toronto, Toronto, Ont.

**Fig. 1.** Numbers of captures per 100 trap-nights (mean  $\pm$  standard error) in three habitat types monitored in Algonquin Park, 1991–1995. Within each species, means with the same letter are not significantly different according to Tukey's post-hoc test ( $P > 0.05$ ) ( $n = 5$  for each habitat).



**Table 1.** Percentages of string (arcsine-transformed) left in each habitat type in the enclosure experiment.

	Sex	Hardwood	Mixed	Coniferous
Redback vole	M	19.08 $\pm$ 2.96	41.31 $\pm$ 1.16	42.01 $\pm$ 2.46
	F	28.56 $\pm$ 4.83	34.29 $\pm$ 5.21	40.63 $\pm$ 6.45
Deer mice	M	28.55 $\pm$ 4.83	34.97 $\pm$ 2.16	40.50 $\pm$ 5.10
	F	32.96 $\pm$ 1.38	36.80 $\pm$ 2.03	35.76 $\pm$ 1.72
Woodland jumping mice	M	29.32 $\pm$ 3.83	34.82 $\pm$ 4.08	40.18 $\pm$ 2.05
	F	29.71 $\pm$ 2.16	34.84 $\pm$ 4.69	40.07 $\pm$ 3.58

**Note:** Values are given as the mean  $\pm$  standard error ( $n = 5$  for all groups).

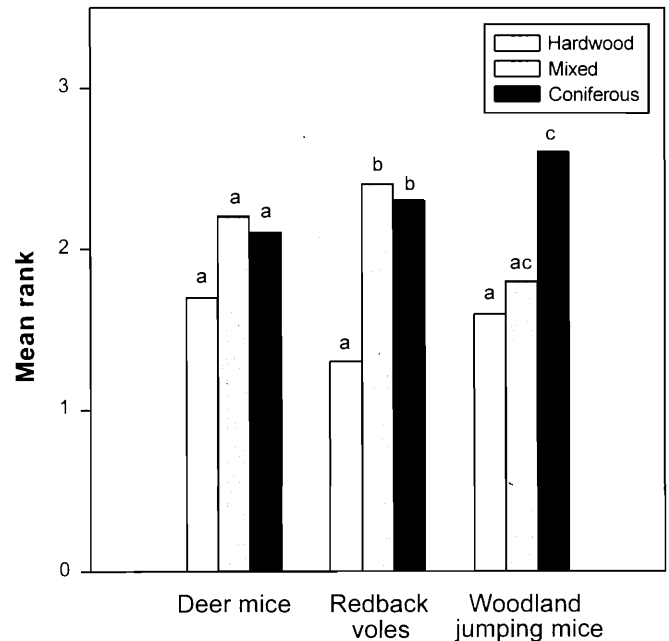
species for analysis, we tested whether the proportions of string (arcsine-transformed) left in each habitat type differed between the sexes for each species. Habitat preferences were ranked and Friedman's test was employed (Zar 1984; White and Garrott 1990). Multiple comparisons were conducted post hoc as described in Zar (1984). A nonparametric method was used because the proportions are inherently non-independent (Aebischer et al. 1993; Manly et al. 1993).

## Results

### Long-term trapping

Mean captures of redback voles were higher in mixed than in hardwood or coniferous forest (Fig. 1;  $F_{[2,12]} = 8.71$ ,  $P = 0.0046$ ). Mean captures of deer mice were higher in hardwood habitats than mixed or coniferous habitats ( $F_{[2,12]} = 21.98$ ,  $P = 0.0001$ ). Mean captures of woodland jumping mice were not significantly different among the three habitat types ( $F_{[2,12]} = 2.10$ ,  $P = 0.1647$ ).

**Fig. 2.** Mean ranks of habitats selected in the enclosure experiment. Within each species, means with the same letter are not significantly different according to post-hoc multiple comparison ( $P > 0.05$ ) ( $n = 10$ ).



### Enclosure experiment

There were no significant differences between males and females of each species (Table 1;  $df = 8$ ,  $t < 1.75$ ,  $P > 0.1$  for all pairings). Multiple application of  $t$  tests gives a higher likelihood of a Type I error (Zar 1984), but this objection should not apply, since any bias would be toward rejection of the null hypothesis. We therefore pooled males and females in further analyses.

Redback voles avoided hardwood substrates and preferred mixed and coniferous substrates in the enclosures (Fig. 2;  $\chi^2 = 7.40$ ,  $df = 2$ ,  $P = 0.025$ ). Deer mice showed no significant substrate preferences ( $\chi^2 = 1.40$ ,  $df = 2$ ,  $P < 0.497$ ). A marginally significant preference for coniferous over hardwood substrates was demonstrated by woodland jumping mice ( $\chi^2 = 5.60$ ,  $df = 2$ ,  $P = 0.061$ ).

## Discussion

Substrates selected by the three species in the enclosure differed from habitats used in the field. Redback voles selected both mixed and coniferous substrates in the enclosure, but in the field, voles were more abundant in mixed forest than coniferous or hardwood forest. Deer mice showed no preference for any substrate type in the enclosure, but were most frequently trapped in maple hardwood habitat. Finally, woodland jumping mice used hardwood less than coniferous substrates in the enclosure, but no differences were found in relative abundance among the three habitat types in the field.

These results seem to support the contention that ecological factors such as competition or predation influence habitat use in deer mice and woodland jumping mice. However, the general concordance between substrate selected in the enclosure and habitat used in the field by redback voles sug-

gests that this species may actually select mixed habitat, as opposed to being constrained to use mixed habitat by competition or predation (Wolff and Dueser 1986).

Using a selection apparatus and a much smaller enclosure, Walker (1964) obtained comparable results in Algonquin Park. He found no distinct selection of either maple or coniferous forest substrate by deer mice despite their abundance in maple forest. He suggested that high densities of mice in the maple forest did not necessarily imply that it was optimal habitat, and thus it was not selected in the experiments. Several trapping studies have found a strong association between small-mammal species and both forest type and ground cover. For instance, of 7 macrohabitat variables, litter depth was the only variable positively correlated with abundance of deer mice, redback voles, and woodland jumping mice in Algonquin Park (Attuquayefio 1995). Other studies have also found both positive and negative associations between our three species and coniferous and deciduous forest types (Kirkland and Griffin 1974; Vickery 1981).

These differences between habitat selection and use can be explained by interactions with heterospecifics. Interspecific competition among the three species is plausible in our study, since woodland jumping mice and deer mice may be displaced from habitats by redback voles (Wrigley 1972; Crowell and Pimm 1976). In our study, redback voles preferred mixed substrate, along with coniferous substrate, in the enclosure and used mixed forest habitats most when free-living. Therefore, the low abundance of both deer mice and woodland jumping mice in mixed forest suggests that redback voles may be inhibiting deer mice and woodland jumping mice from selecting some habitats. Predation, and its effects on activity, movement, and location of prey, may also explain the differences between habitats selected and used in our study. Prey species may shift habitat use in the presence of a potential predator (Kotler et al. 1991; Dickman 1992; Lagos et al. 1995). Theoretical work has suggested that predation can interact with competition and cause shifts in habitat use by changing densities of competitors and thus changing resource abundance (Kotler and Holt 1989).

The general preference for mixed and coniferous habitat over hardwood forest by all three species may be due to predator avoidance. All three species were observed within the enclosures prior to the experiment. Movement by animals through hardwood leaf litter produced much more noise than movement through coniferous leaf litter. Avoidance of noise may be a factor in avoiding predation, particularly in small mammals, since primary nocturnal predators such as owls use sound as a cue (Burton 1978).

The use of two different methods to measure habitat use and preference may have confounded our results. Unfortunately, spool tracking could not be done with field populations to measure habitat use, since spools carry 70–100 m of string and habitat patches can be larger than this. Trapping could have been done in enclosures, but constructing enclosures large enough for trapping, and transplanting enough forest-floor substrate to construct habitats within the enclosures, would not have been possible. These differences in methodology required differential treatment of animals (i.e., anaesthetized versus undisturbed animals). These caveats aside, we believe our results to be reasonably robust, but further study should be done to test for potential differences

among methods of measuring habitat use (i.e., trapping, radiotelemetry, spool-tracking, etc.).

Although no concrete suggestions regarding the mechanisms behind distribution of small mammals among habitats, can be offered on the basis of the results of this study, it does offer an experimental protocol that may be more successful than population- or community-based studies in determining causal mechanisms. Much of the literature is focussed on trapping studies and the use of regression and discriminant analyses to differentiate between habitat selection and habitat use (e.g., Crowell and Pimm 1976; Dueser and Hallet 1980; Hallet et al. 1983; Rosenzweig et al. 1984). Although individually based, experimental approaches have been employed (e.g., Dooley and Dueser 1996), the literature is replete with population approaches to habitat selection. Many of these, particularly those investigating temperate small-mammal communities, lacked controls and replication (e.g., Brown and Batzli 1985), which are necessary for proper experimental design (Hurlbert 1984; Hairston 1989), although appropriate designs have been employed in some cases (e.g., Abramsky et al. 1992; Haken and Batzli 1996). The use of enclosures can be an important tool for explaining patterns in ecological systems and offers a legitimate compromise between statistical rigour and realism (Hairston 1989). For instance, results from comparably sized enclosure experiments and field investigations have been used to examine vertical nest-site segregation within and between deer mice and syntopic white-footed mice (*Peromyscus leucopus*) (Harney and Dueser 1987; Dooley and Dueser 1996). The typical home-range size for all three of our species is approximately 1 ha (Nowak 1991), which is considerably smaller than the enclosures. Despite this, habitat preferences would likely still be evident in enclosures smaller than an individual's home range (Schoener 1986). The experimental protocol described here allows for replication and controls while trying to discern the effects of both inter- and intraspecific competition and predation on habitat distribution.

We conclude that interspecific competition and predation can both produce the patterns we observed. Further work to test these hypotheses will involve introducing two heterospecifics into an enclosure and tracking habitat use by both animals. We will determine whether a shift in habitat use occurs when a competitor is present. Using the enclosures, we will also test the hypothesis that animals reduce their movements through hardwood leaf litter because of excess noise by "dampening" the sound created by small mammals while moving in maple-leaf litter.

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