
The impact of predation on burrow use by Arctic ground squirrels in the boreal forest

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In sedentary animals, the choice of a suitable home site is critical to survival and reproductive fitness. However, habitat suitability may vary with predation risk. We compared habitat use of Arctic ground squirrels (*Spermophilus parryii plesius*) living in the boreal forest under conditions of fluctuating predation pressure. In our study area, predators show ten-year cycles in numbers that track that of their primary prey, the snowshoe hare (*Lepus americanus*). In 1993, we compared burrows that continued to be occupied following the period of intense predation during the hare decline of 1990–1992 with those that became vacant, and with random locations. We contrasted these sites to those in a predator enclosure where predation pressure was minimized. Burrows on control sites were located on sloped sites with high visibility. Burrows that remained occupied during the period of intense predation were more likely to be in open areas with fewer fallen trees than burrows that became vacant. We used discriminant functions derived from the control sites and found that 89% of the burrows on the predator enclosure were classified as being similar to the random locations on control sites. We conclude that the distribution of Arctic ground squirrels in the boreal forest is a direct function of predator presence.

Keywords: Arctic ground squirrels; burrow; boreal forest; predation; habitat use; discriminant function analysis

1. INTRODUCTION

A critical factor determining the fitness of an individual is finding a suitable place to live (Cody 1985). The cues it uses in site selection may include physical structures necessary for construction of nests or dens (Rhodes & Richmond 1985) or sufficient food for reproduction (Arcese & Smith 1988; Wiehn & Korpimäki 1997). However, even if a site passes these tests, exposure to predation may ultimately determine a species' distribution or abundance (Lawton & Woodroffe 1991) by directly removing prey or indirectly forcing them to live elsewhere (Doncaster 1992). Prey forced to select alternative sites that offer increased protection may encounter a cost of reduced food quantity or quality (Hik 1995; Holomuzki & Hoyle 1990). Alternatively, prey can endure high predation risk at a site by increasing their vigilance but in so doing, trading off time that should be spent foraging (Bachman 1993; Lima 1987). However, for vigilance to be most effective, prey need to find a habitat that maximizes visibility. However, when predation pressure varies, the need for protection or vigilance should also vary, and this may ultimately affect the quality of the habitat. Our objective was to determine how changing predation pressure affects the distribution of Arctic ground squirrels (*Spermophilus parryii plesius*) in the boreal forest by comparing their habitat use during temporal and experimental changes in predation pressure.

Arctic ground squirrels are found in mainland arctic tundra and the northern boreal forests of Canada and

Alaska (Howell 1938). They have an underground burrow system that serves as a hibernaculum in winter and a shelter from adverse weather and predators in summer. The summer burrow system usually shelters a female squirrel for her entire life, whereas all males disperse from their burrows annually (Lacey 1991). Carl (1971) and Batzli & Sobaski (1980) suggested that predators were unimportant in the tundra environment and that populations were stable and limited by food, spacing behaviour and burrow availability. In the boreal forest of the south-western Yukon, ground squirrel populations fluctuate in synchrony with the ten-year cycle in abundance of snowshoe hare (*Lepus americanus*) and its predators (Boutin *et al.* 1995). Here, ground squirrels must cope simultaneously with two groups of predators with different hunting techniques: avian predators hunt mainly in open areas (e.g. red-tailed hawks *Buteo jamaicensis*, McInville & Keith 1974; and great-horned owls *Bubo virginianus*, Rohner & Krebs 1996); whereas mammalian predators can hunt in both open and forested areas (coyotes *Canis latrans*, Bekoff & Wells 1986; and lynx *Lynx canadensis*, Murray *et al.* 1995; O'Donoghue *et al.* 1998). When hare numbers declined from 1990 to 1992, survival rates of ground squirrels decreased from 70% to 20% over the active season (Hubbs & Boonstra 1997). Our study was conducted in 1993, when ground squirrel populations had declined to their lowest densities after this period of intense predation (Byrom 1997), leaving many burrows vacant.

We tested the hypothesis that mammalian predators control where Arctic ground squirrels successfully live in the boreal forest in two ways. First, we compared the

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habitat characteristics of burrows on control areas that continued to be occupied with those that had become vacant. If there is selection against squirrels living in poor-quality habitats, then burrows remaining occupied should be located in qualitatively safer habitats than burrows from which occupants had disappeared. Second, we compared the habitat characteristics of all burrow sites in a mammalian predator enclosure with those from control areas. If selection pressure is reduced within the enclosure, burrows should be located independently of habitat characteristics.

2. METHODS

The study was located within the Shakwak Trench east of Kluane Lake in the south-western Yukon Territory, Canada (61°N, 138°W). There are four major vegetation types in this valley: white spruce forests (*Picea glauca*) cover about 50% of the area and have an understory of willow (*Salix* spp.) and birch (*Betula glandulosa*); shrub meadows of willow and birch cover 33%; grass meadows cover 7% (Boutin *et al.* 1995); and trembling aspen (*Populus tremuloides*) stands (10%) are sparsely distributed among the three main vegetation types (C. J. Krebs, personal communication).

Our investigation was set up as part of the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* 1995) designed to investigate the community structure of the boreal forest. We used three of the experimental treatments from this project (all within 2 km of each other): an unmanipulated 10 ha control; a 36 ha control that was provided with supplemental food but not protected from predators; and a 1 km² predator enclosure treatment, which excluded large mammalian predators (lynx and coyotes) but allowed squirrels to move freely in and out (see Krebs *et al.* (1995) for details on treatments). Population densities ranged from 0.7 ha⁻¹ (controls) to 1.6 ha⁻¹ (predator enclosure) to 3.0 ha⁻¹ (food-supplemented).

From April to September 1993 we determined whether all ground squirrel burrows on a 10 ha area within each treatment were occupied or vacant. We live-trapped squirrels every two weeks using 14 cm × 14 cm × 40 cm traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) and monitored squirrels by radio telemetry every week using radio collars (PD-2C, Holohil Systems, Carp, Ontario). Each burrow was considered to be occupied if a squirrel was repeatedly caught or located there by radio telemetry (≥ five times), or vacant if a ground squirrel was rarely captured there (less than five times out of approximately 25 possible captures), or the opening was clogged with debris. Because vacant burrows persist for many years, owing to the cold and dry nature of the climate, we used only burrows that we knew were occupied during 1991 when density was highest (Hubbs & Boonstra 1997).

We compared the habitat structure of all burrows to random sites on the trapping grids. Coordinates for random sites within the trapping grids were derived using a random number generator and were rejected if they fell within 15 m of a burrow site. Habitat was assessed for 25 occupied burrows (control = 16, predator enclosure = 9), 22 vacant burrows (control = 15, predator enclosure = 7) and 44 random locations (control = 35, predator enclosure = 9). Sample sizes among treatments varied because we limited our study to burrows known to be active in previous years. Habitat was assessed within a 15 m radius of each burrow or random location and these were classified with the following habitat variables.

- (i) Structure: beneath a standing spruce, deadfall (fallen dead spruce or stump), shrub, or out in the open.
- (ii) Slope: sloped if incline > 10° or flat if < 10°.
- (iii) Dominant spruce size: small < 8 cm diameter, medium > 8 cm and < 15 cm diameter, or large > 15 cm diameter. If < 85% of trees were a single size category, the area was classified as mixed.
- (iv) Deadfall: amount of dead spruce trees lying on the ground. Deadfall was ranked on a scale of 0 (no deadfall) to 4 (high deadfall).
- (v) Open: percentage of open habitat (± 10%) not covered by spruce, deadfall or shrubs.
- (vi) Visibility: a 0.7 m × 0.04 m stake painted black and tan in alternate 10 cm sections was held both perpendicular and horizontal to the ground at 70 cm (approximate head height of a lynx or coyote) at intervals 5 m, 10 m and 20 m along a random bearing from an observer situated at the site (method adapted from MacHutchon & Harestad (1990)). The observer recorded the percentage (± 5%) of the stake seen from a position of 27 cm (approximate eye level of alert ground squirrel) above the highest burrow mound. An average visibility was calculated for each distance interval from three random directions.

(a) Statistical analysis

In all univariate tests we followed Zar (1984) and Sokal & Rohlf (1995). We used the following programs: Statview (Roth *et al.* 1994) for log-linear models (*G*-test); SuperANOVA (Gagnon *et al.* 1991) for ANOVA and post-hoc tests (Tukey–Kramer); G-Power (Buchner *et al.* 1997) for power analysis; and Statistica (Statsoft 1994) for multivariate statistics using methods described by Tabachnick & Fidell (1996). Prior to analysis, all habitat data were screened for errors, missing values and outliers. Prior to pooling, we tested all habitat predictors for differences between the two control sites using ANOVA for continuous data and *G*-tests for categorical data with $\alpha = 0.003$ after Bonferonni correction. We give *p*-values between 0.05 and 0.10 and infer that these may be biologically, though not statistically, significant, possibly because low sample sizes reduced power in some of our results (Yoccoz 1990).

Careful checks were made for departures from normality, multivariate outliers and collinearity. None were found, except for the distributions for visibility, which were successfully normalized by square-root transformation. A stepwise discriminant function analysis was performed to assess the prediction of membership in the three site classifications (occupied, vacant and random) on control areas using the eight habitat predictors. Each variable with $F \geq 1$ was entered sequentially into the analysis in order of greatest contribution to discrimination among groups. To find the approximate *F*-ratio for the discriminant function analysis, we calculated degrees of freedom according to equations in Tabachnick & Fidell (1996, p. 516). We restricted our interpretation of each discriminant function to those predictor variables that had correlations with the function that were greater than 0.32 (explaining 10% of the variance). Variables with correlations greater than 0.63 (40% of the variance) are considered to be very good predictors (Comrey 1973).

3. RESULTS

(a) Burrow characteristics on the control sites

There were no differences between the control areas in any of the continuous variables for each of the site

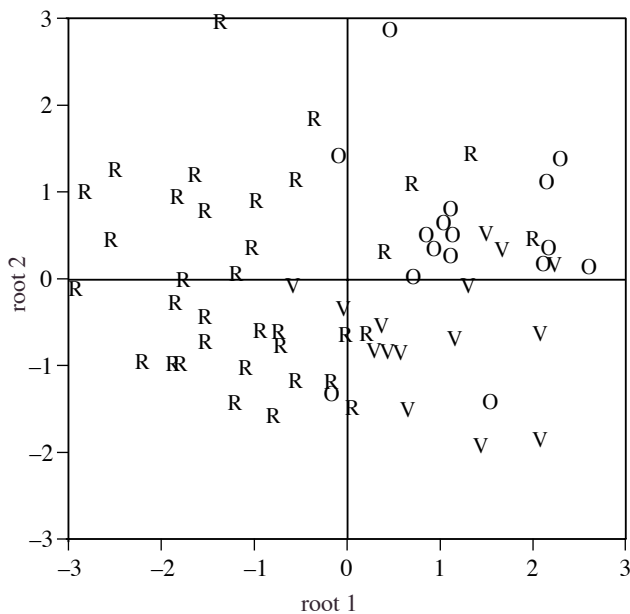


Figure 1. Canonical scores for two discriminant functions derived from five habitat variables describing occupied burrows (O), vacant burrows (V) and random locations (R). The first discriminant function (root 1) separates burrow locations from random locations ($\chi^2 = 56.78$, d.f. = 10, $p < 0.001$). The second discriminant function (root 2) spreads but does not significantly separate vacant burrows from occupied ones ($\chi^2 = 8.49$, d.f. = 4, $p = 0.08$).

classifications (occupied, vacant and random) (visibility and open: all $p > 0.05$). For the categorical variables there were no differences in frequency of slope (all $p > 0.3$) and deadfall (all $p > 0.03$). Only spruce size differed between control sites, but for random locations only ($p < 0.001$). Since burrow habitats were similar between the high-density control and low-density control, then differences in population density between the sites did not influence where squirrels live. After pooling both control areas, sites were best discriminated by visibility at 10 m, slope, deadfall, open and spruce size ($F_{10,118} = 6.99$, $p < 0.001$). The other variables (burrow structure, and visibility at 5 m and 20 m) had $F < 1$ and were deleted from the analysis. We determined how well our discriminant function fitted our classification of burrow sites by calculating the probability that sites assigned a classification by the discriminant function (predicted) were the correct classification (observed). We found that the discriminant function correctly classified 89% of the random locations, 60% of the vacant burrows and 81% of the occupied burrows. Out of the vacant burrows incorrectly classified, 27% were classified as occupied burrows and 13% as random sites.

There was a significant association between burrow groups and predictors ($\chi^2 = 56.78$, d.f. = 10, $p < 0.001$). After removal of the first function, association using the second function was nearly significant ($\chi^2 = 8.49$, d.f. = 4, $p = 0.08$). The first and second discriminant functions accounted for 89% and 11%, respectively, of the variation in discriminating among groups. The first discriminant function (root 1) nearly separated random locations from locations with burrows, and the second discriminant function (root 2) tended to separate vacant burrows from occupied burrows (figure 1).

Table 1. Results of discriminant function analysis showing pooled within-group correlations of canonical roots and significance level of variables contributing to the discriminant function. Root 1 and root 2 are the first and second discriminant functions

variable	correlation of predictor variables with discriminant functions		$F_{2,59}$	p
	root 1	root 2		
visibility at 10 m	0.78	-0.10	14.67	< 0.001
slope	0.60	0.18	7.30	0.001
deadfall	-0.07	-0.67	2.80	0.07
open	0.16	0.47	1.44	0.2
spruce size	-0.14	0.39	1.08	0.3

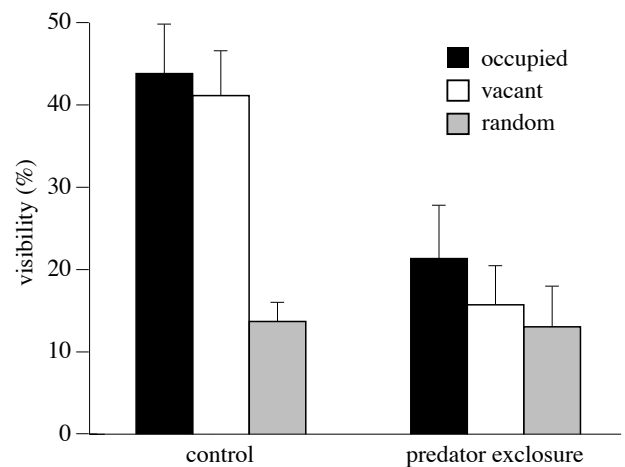


Figure 2. Comparison of visibility at 10 m from occupied and vacant burrows of Arctic ground squirrels and from random locations on control areas with those on the predator exclusion.

The primary predictors (loadings ≥ 0.50) (i.e. 25% variance) that best discriminated between random locations and locations with burrows (root 1) were visibility at 10 m and slope (table 1). Visibility at 10 m differed significantly among the three sites ($F_{2,63} = 23.15$, $p < 0.001$) (figure 2). Visibility at occupied burrows ($43.6 \pm 6.0\%$) and vacant burrows ($40.9 \pm 5.4\%$) did not differ (Tukey-Kramer: $p > 0.05$) but both had greater visibility than random locations ($13.6 \pm 2.2\%$) (Tukey-Kramer: $p < 0.05$). Burrows were significantly associated with slopes (occupied and vacant burrows pooled: $G = 20.52$, d.f. = 1, $p < 0.001$), with 74% of burrows on slopes whereas only 20% of random sites were on slopes.

The second discriminant function (root 2), which included deadfall, percentage open and spruce size, only weakly characterized sites. However, we still explored each of these predictors univariately because of the tendency for separation between vacant and abandoned burrows (figure 1). There was only one case of deadfall index > 2 in each of the vacant and occupied burrow

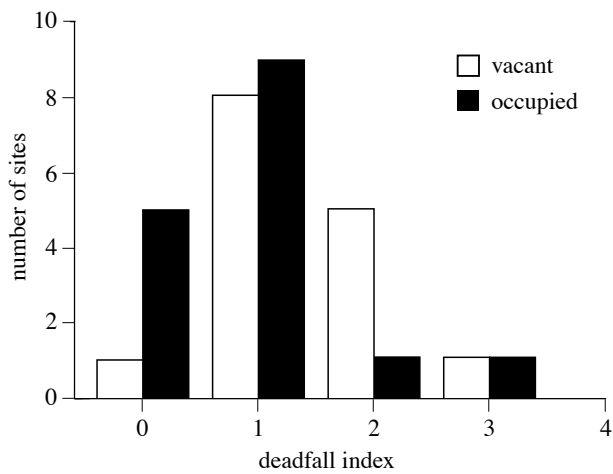


Figure 3. Comparison of deadfall indices within 15 m of occupied Arctic ground squirrel burrows with that of vacant burrows on control areas.

classifications and so these two cases were pooled with a deadfall index of 2. Occupied burrows tended to have more deadfall than vacant burrows ($G = 5.03$, d.f. = 2, $p = 0.08$) (figure 3). On our sites, small spruce were absent and large spruce were rare (one case) so the large and medium categories were pooled before analysis. The proportion of burrows in medium spruce habitat did not differ significantly between occupied burrows (47%) and vacant burrows (58%) ($G = 0.36$, d.f. = 1, $p = 0.55$).

(b) *Burrow characteristics on the predator exclusion treatment*

We used the discriminant functions from the control areas to predict the sites on the predator exclusion that we had already classified as occupied burrows, vacant burrows and random sites. The predicted classifications on the predator exclusion treatment differed from our observations ($\chi^2 = 16.05$, d.f. = 2, $p < 0.001$). Nearly all (89%) random locations were correctly predicted and thus were similar to those on controls. None of the occupied burrows and only 14% of the vacant burrows was correctly predicted. Nearly all burrows (88%, $n = 16$) were predicted as random locations. Thus, while habitat characteristics of random locations were similar between the control and the predator exclusion, burrow locations were not. Burrows on the exclusion treatment shared more habitat characteristics with random locations than they did with burrows on control areas.

To determine the nature of the similarity between burrows and random locations we explored each variable separately. Occupied burrows on the predator exclusion had less than half the visibility at 10 m than those on controls ($F_{1,23} = 7.39$, $p = 0.01$) (figure 2), though visibility at random locations was similar on both areas ($F_{1,42} = 0.31$, $p = 0.58$) (figure 2). Nearly twice as many occupied burrows occurred on slopes on control sites (81%) than on the predator exclusion (44%) ($G = 3.54$, d.f. = 1, $p = 0.06$). Similarly, nearly twice as many random locations occurred on slopes within control sites (20%) than on the predator exclusion (11%) ($G = 0.42$, d.f. = 1, $p = 0.52$), but our ability to detect a difference was low (power $(1 - \beta) = 0.34$). Thus, differences in frequencies of

burrows in slopes between the controls and the predator exclusion were a function of available sloped habitat and were independent of predators. We pooled deadfall indices 2, 3 and 4, owing to the low frequency of high deadfall aggregation. Burrows on control sites were slightly more likely to be located in areas of no (index = 0) or very little (index = 1) deadfall (31% and 56%, respectively, for controls versus 11% and 33% for the predator exclusion: $G = 5.39$, d.f. = 2, $p = 0.07$). We did not find a significant difference between the treatments for random sites ($G = 3.67$, d.f. = 2, $p = 0.16$) despite a high power > 0.99 . Both treatments had a similar percentage of open area around occupied burrows ($F_{1,23} = 0.07$, $p = 0.80$) (control = $62.5 \pm 5.4\%$; predator exclusion = $64.4 \pm 2.4\%$) and for random locations ($F_{1,42} = 0.78$, $p = 0.38$) (control = $52.7 \pm 2.6\%$; predator exclusion = $57.8 \pm 5.2\%$). We could not compare spruce size indices between treatments due to low frequencies for some categories but we could compare random and occupied locations within treatments. Occupied and random locations on either treatment were similar (control: $G = 0.36$, d.f. = 2, $p = 0.84$; predator exclusion: $G = 0.23$, d.f. = 1, $p = 0.63$). Therefore, reduced visibility was the primary habitat characteristic creating the similarity between burrow locations on the predator exclusion and random locations on both sites. Burrows on control areas were more often found in sites with high visibility compared with random locations and burrows on the predator exclusion.

4. DISCUSSION

Our results indicate that predation influences the distribution of Arctic ground squirrels in the boreal forest by selecting against ground squirrels living in habitat that reduces their ability to detect predators. All ground squirrel burrows on control sites were located on sloping sites with high visibility (at 10 m). After a three-year period of intense predation, burrows that remained occupied were more likely to be in more open areas with less deadfall than burrows that became vacant (figure 3). When mammalian predation was experimentally reduced (predator exclusion), burrows were located at random with respect to local habitat structure. Thus, Arctic ground squirrels would occupy a much broader distribution of habitats in the boreal forest were it not for the presence of mammalian predators.

We discuss two caveats that could affect our interpretation. First, density on the predator exclusion was approximately twice that of unmanipulated control sites (Karels *et al.* 1999), and perhaps crowding forced ground squirrels to occupy suboptimal sites. However, the food-supplemented control site had densities twice that of the predator exclusion and four times that of the other control in otherwise similar habitat. Burrow site habitat was not influenced by density since burrows on the high-density food addition site were located in similar habitat to those on the lower-density control sites. When densities were high, squirrels increased sharing of burrows (Karels *et al.* 1999) thus limiting the amount of habitat used. Therefore, habitat use on the predator exclusion was not a result of social interactions. Our second caveat deals with a pseudo-replicated experimental design. We had only single treatments from which we treated burrow sites

as replicates, assuming each burrow as an independent sample. Our study, as well as others that have used these same experimental areas (e.g. Krebs *et al.* 1995; Hubbs & Boonstra 1997; Karels *et al.* 1999), have traded replicated design for larger scale and long-term manipulations, a common problem with whole ecosystem experiments burdened with limited funding (Carpenter *et al.* 1995).

Visibility, which was the most important variable on our control sites, is a critical factor affecting rodent distribution. For some situations, dense vegetative cover may protect prey from visual exposure to predators (Brown *et al.* 1988; Kotler *et al.* 1991). For other situations, dense cover may allow the predator to approach prey undetected. In the latter situation, prey need a clear line of sight to detect approaching predators (Cassini 1991) and this has been demonstrated especially for ground squirrels (MacHutchon & Harestad 1990; Schooley *et al.* 1995; Travis & Armitage 1972). Cassini & Galante (1992) found that wild guinea-pigs (*Cavia aperea*) solve the trade-off between foraging and predation risk by using a shelter when inactive and by foraging within groups when far from cover (Cassini 1991). Unlike guinea-pigs, ground squirrels construct their own shelter (i.e. burrows) in areas that maximize food availability and thus can reduce the time spent vigilant since the distance to escape to shelter is small (Holmes 1984). They can also reduce vigilance time by foraging in areas where predators can be detected at greater distances (Armitage 1982; Carey & Moore 1986). In our study area in 1994, lynx were twice observed approaching ground squirrels to within 5 m on an open hillside (T. Karels, personal observation). In both cases, the squirrels were aware of the lynx, as indicated by their alarm calls, and subsequently escaped to their burrows. Thus, a lynx's success rate is probably reduced considerably when seen by a ground squirrel. Habitat that reduces the probability of predator detection increases the risk of predation for ground squirrels (Balph & Balph 1966; Slade & Balph 1974). Yellow-bellied marmots (*Marmota flaviventris*) abandon their burrows when vegetation grows high (Svendsen 1976) and Townsend's ground squirrels (*S. townsendii*) spend more time vigilant in habitats with low predator detection distances (Sharpe & VanHorne 1998). To increase their detection distance, ground squirrels climb structures such as rocks, burrow mounds, fence posts and trees (Hubbs *et al.* 1996; MacHutchon & Harestad 1990; Sherman 1985; Tyser 1980). Therefore, ground squirrels can assess predation risk in various habitats and minimize it by selecting sites with minimal visual obstruction.

Slope was an important feature in determining burrow locations in our study but was independent of predation. Ortega (1987) found also that slope influenced the location of rock squirrel (*Spermophilus variegatus*) burrows. The slope of the terrain is important for creating burrows because of the drier soil conditions resulting from quick drainage and earlier snow melt on south-facing slopes (Shaw 1925, 1926; Svendsen 1976).

There are three predator-related mechanisms that could prevent ground squirrels from occupying a greater range in habitat types: first, by causing squirrels to avoid particular habitats; second, by removing squirrels from particular habitats; and third, by lowering the fitness of squirrels living in a particular habitat. Ground

squirrels show phenotypic plasticity in life-history patterns (Dobson & Kjelgaard 1985; Dobson & Murie 1987) and our study shows that Arctic ground squirrels exhibit plasticity in habitat choice. Squirrels on the predator enclosure constructed and lived in burrows in a greater variety of habitat types than those on controls, and thus the latter avoided these habitat types. Thus this flexibility in habitat choice stands in contrast to species such as the prairie deer mouse (*Peromyscus maniculatus bairdi*), which is genetically programmed to live in only one habitat type, the grassland (Wecker 1963). Phenotypic plasticity may be one reason why Arctic ground squirrels, which are predominately found in tundra habitats (Howell 1938), have successfully colonized northern regions of the boreal forest. However, in this region, ground squirrel populations are subjected to periodic intense predation when hares become scarce and predators are still abundant (Hubbs & Boonstra 1997). Predators may have removed individuals from risky habitats in our study, which may explain the tendency in habitat differences between occupied and unoccupied burrows. Predators may have directly removed pre-reproductive individuals from a burrow or they may have indirectly prevented individuals from reproducing (Karels *et al.* 1999), leaving the burrow without successors since female squirrels inherit their burrows from their mothers (Lacey 1991). The most likely scenario for our observed effects is a combination of these mechanisms. We do not know the proportions in which these mechanisms effect squirrel habitat use, but our results show that the combined effect substantially determines where ground squirrels exist in the boreal forest.

The interaction between site quality and predation may have important effects on population dynamics (Rodenhouse *et al.* 1997). Burrows in low-risk habitat may serve as refugia from which squirrels reoccupy other areas following the decline of the predators. In our study area, the key predators (lynx and coyotes) are not abundant long enough to cause local extinction of ground squirrels, as they quickly disappear from the system when hares become scarce (Boutin *et al.* 1995; O'Donoghue 1997). When predator densities were at very low levels, ground squirrels increased rapidly in numbers (Byrom 1997; Karels *et al.* 1999) and in distribution throughout the habitat, as we observed on controls and on the predator enclosure treatment. The fluctuation in Arctic ground squirrel abundance during the hare cycle may be partly dependent on the expansion of habitat use when predators are scarce and the contraction of habitat use when predators are abundant.

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