

## HABITAT-MEDIATED VARIATION IN PREDATION RISK BY THE AMERICAN MARTEN

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**Abstract.** The probability of prey encounter, attack, capture, and kill are often hypothesized to depend on habitat structure, but field evidence in terrestrial systems is rare. We tested whether predation efficiency by the American marten (*Martes americana*) and fear of predation by their primary prey, the red-backed vole (*Clethrionomys gapperi*), differed between 20- and 50-year-old regenerating forest stands and older uncut stands. Our results showed that the frequency of prey encounter, prey attack, and prey kill were higher in old uncut forests, despite the fact that small-mammal density was similar to that in younger logged forests. These differences in predation efficiency were linked to higher abundance of coarse woody debris, which seems to offer sensory cues to martens, thereby increasing the odds of hunting success. Red-backed voles in regenerating forest stands exhibited increased wariness compared to voles living in old uncut forest, suggestive of a behavioral response to habitat-mediated variation in predation risk.

**Key words:** *Clethrionomys gapperi*; coarse woody debris; forest; giving-up density; habitat complexity; hunting; *Martes americana*; *Microtus pennsylvanicus*; predator; prey; search efficiency.

### INTRODUCTION

Ecological models commonly use prey abundance as a measure of predator habitat suitability and as a predictor of home range size, diet, and fitness. Prey presence does not, however, guarantee prey availability to predators. The probability of prey encounter, attack, capture, and kill may depend on the degree of structural complexity of physical environment. Structural habitat complexity may reduce the efficiency of searching predators, by providing physical refugia for prey, making prey less conspicuous, or slowing predator search and pursuit speeds. Alternatively, increased structural complexity of habitats could increase prey vulnerability, provided that prey individuals are associated with specific structural elements that predators use to enhance their search efficiency (Bell 1991). Despite the intuitive appeal of this hypothesis, field tests of the effect of habitat complexity on predator search efficiency are surprisingly rare, especially in terrestrial environments (Crowder and Cooper 1982, Anderson 1984, Savino and Stein 1989).

Here we compare the search efficiency of American martens (*Martes americana*) in regenerating forest stands vs. older uncut old forest stands near Ear Falls, Ontario, Canada. Structural complexity is often reduced in regenerating forests compared to in older forests, particularly in the amount of coarse woody debris

(Clark et al. 1998). We accordingly tested two competing hypotheses. If coarse woody debris provides small mammals with structural refuge, then marten should encounter, attack, and kill small mammals more frequently in regenerating forest, where there is less coarse woody debris. Small mammals should be more vulnerable, and consequently be used more by marten in logged forests. Alternatively, if coarse woody debris provides marten with sensory cues to the location of small mammals, then marten should encounter, attack, and kill small mammals more frequently in old uncut forests where coarse woody debris is abundant. Small mammals should be more vulnerable, and consequently be used more by marten in old uncut forests.

We also used “giving-up densities” to assess the perception of predation risk by red-backed voles (*Clethrionomys gapperi*), the numerically dominant small mammal in our study area and the most common species in marten diets. The giving-up density is the amount of food remaining in an experimental patch when an individual ceases foraging, corresponding to the forager’s quitting harvest rate (Brown 1988). Optimal foragers should quit patches when the rate of energy gain just balances the missed-opportunity cost and predation risk (Brown 1988). Spatial variation in predation risk can be assessed by comparing giving-up densities from risky vs. safe microsites (Kotler et al. 1991, Kotler 1997, Morris 1997, 2000), with fear of predation proportional to differences in giving-up density between safe vs. risky microsites. If coarse woody debris provides structural refuge and therefore decreases the vulnerability of small mammals to

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martens, then red-backed voles should show greater fear in logged forest stands, where there is less coarse woody debris. Alternatively, if coarse woody debris provides marten with sensory cues and increases the vulnerability of small mammals, then red-backed voles should show greater fear in old uncut forest where coarse woody debris is abundant.

#### METHODS

The study area consisted of two boreal forest landscapes near Ear Falls, Ontario, Canada, (50°38' N, 93°13' W), described in detail in Thompson et al. (2007). The old uncut landscape was ~1000 km<sup>2</sup>, with a canopy dominated by jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and trembling aspen (*Populus tremuloides*) of 80–120 year-old fire origin. The younger regenerating logged landscape consisted of two noncontiguous areas of ~200 and 800 km<sup>2</sup>. Both areas of regenerating forest had primarily been clear-cut, with some selection harvesting, 20–55 years ago but also contained ~10% recent (<8 years) clear-cuts, and 10% residual, old uncut forest. Forest canopy in the regenerating landscape was dominated by jack pine, black spruce, balsam poplar (*Populus balsamifera*), trembling aspen, balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*).

We measured habitat features (abundance of coarse woody debris, subnivean access, prey abundance) at the stand level for all age–forest type combinations determined from digital forest resource inventory (FRI) maps, hereafter called stand types. We made all comparisons between regenerating and uncut forests at the home range level. For each habitat feature, we estimated abundance in marten home ranges by multiplying the proportional area of stand types in home ranges by the corresponding stand-level abundances, and summing over all stand types. We measured marten prey choice and hunting success directly at the home range level.

We defined coarse woody debris as all downed woody material ≥10 cm in diameter and measured its volume according to McRae et al. (1979), with five transects per stand in 5–9 replicates of each stand type and increased the sample to 10 transects, if the coefficient of variation following five transects exceeded 30%. Logs in early decay classes (1–3) (Maser et al. 1979) were solid wood and contributed to habitat structure, while logs in advanced decay classes (4–5) were mostly on or in the duff layer and contributed less to habitat structure. We tested for differences in the abundance of coarse woody debris for classes 1–3 and classes 1–5 between regenerating and uncut forest with MANOVA.

Access to the subnivean space is created by snow settling around coarse woody debris, trunks of standing trees, low branches of young trees, and animal-constructed tunnels. We defined subnivean access as any hole in the snow large enough and deep enough for marten to enter (diameter ≥10 cm) to the forest floor.

We counted subnivean access points within 1 m of 1-km transects in 4–6 replicates of each stand type to provide an estimate of relative availability to marten. We measured snow depth at 250-m intervals along these transects, and estimated a mean snow depth for each transect. We tested for differences in the relative availability of subnivean access between regenerating and uncut forest with ANCOVA using snow depth as a covariate.

We captured small mammals in Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, USA) in two trap sessions straddling winter 2002 (fall 2001, 22 September–22 October; and spring 2002, 21 April–31 May). We trapped one line per stand over five replicates per stand type. Trap lines consisted of 10 stations at 10-m intervals, with two traps per station placed 1 m apart. Traps were baited with peanut butter and rolled oats, and checked on each of three consecutive mornings. We estimated small-mammal densities for winter 2002 as the mean of fall 2001 and spring 2002 catch per unit effort.

We captured marten in Tomahawk live traps (Models 106 and 107, Tomahawk Live Trap, Tomahawk, Wisconsin, USA) throughout the study. Marten were sexed, weighed, and fitted with a 30-g radio collar (model MI2, Holohil Systems, Carp, Ontario, Canada). The first lower premolar tooth was extracted for aging by cementum annuli counts (Strickland and Douglas 1987).

We located radio-collared marten opportunistically with radiotelemetry daily to weekly from truck, snowmobile, aircraft, and on foot. Locations were determined using the Tukey maximum likelihood estimator (Lenth 1981) in the program Locate II (Nams 1990). To reduce the chance of placing marten in the wrong stand, we included a location in home range estimations only if the area of its 95% error ellipse was <0.5 km<sup>2</sup>. We downloaded locations to ArcView (version 3.2, Environmental Systems Research Institute, Redlands, California, USA) and estimated home ranges with the “Animal Movement Extension” (Hooge and Eichenlaub 1997). We used the 100% minimum convex polygon method because it represents space available to the animal independent of the amount of use.

We quantified marten hunting success by snow-tracking 34 radio-collared marten for a total of 100 km. Tracking effort was allocated similarly among landscape, sex, and age (regenerating, 4 female adults, 5 female juveniles, 4 male adults, 5 male juveniles; uncut, 6 female adults, 3 female juveniles, 4 male adults, 4 male juveniles). We followed radio signals until we intercepted fresh tracks, then backtracked marten (mean 2.95 km) until the trail or daylight was lost. We counted subnivean access points within 1-m lateral distance, subnivean investigations, and the number of prey encountered, attacked, and killed along marten search paths. Subnivean access quantified along marten search paths provided an estimate of those selected by marten. We chose 1 m for inclusion of subnivean access counts

as a conservative sensory range based on observed reaction distances of marten. We determined marten diet by identifying prey remains from kill sites and in scat contents, following the key of Thompson et al. (1987).

Marten encounter small mammals below the snow. Fresh snow, wind, and melt quickly erase small-mammal sign in the snow. We accordingly assumed the spatial proximity of marten tracks with small-mammal sign (tracks, urine, feces) to be a useful indicator of potential prey encounters. We tested the presumed relationship between small-mammal sign and small-mammal presence by placing live traps at subnivean (below snow) access points where small-mammal sign was observed. Live-captures of small mammals were correlated with the presence of sign (62 of 80 trap nights). We could distinguish subnivean prey investigations from actual attacks on small mammals only when kills were made. Therefore, we counted the number of subnivean access points that marten entered and used this as a pooled estimate of subnivean prey investigations and attacks. Small-mammal kills were indicated by the presence of blood, viscera, tufts of hair, or a marten body print in the snow where small mammals were eaten. Two or more of these signs were present at every kill site. We quantified the quality of subnivean access points according to the proximity of small mammals and use by marten as the number of small-mammal encounters, attacks, and kills per point. While we could not absolutely ascertain whether or not marten ate prey in the subnivean zone, we suspect that such activity may have been rare because of the consistent observation of marten emerging from holes to eat on the snow surface.

Marten hunting success may differ with age if younger, inexperienced marten have higher search and handling times, and with sex if larger prey are exclusively available to males, which are 35–40% larger than females (Thompson and Colgan 1990). Further, deep snow may limit access to subnivean prey (Hargis and McCullough 1984). Therefore, we compared the number of subnivean access points selected by marten, the number of small mammals encountered, attacked, and killed per kilometer and per access point, total small-mammal availability, and strike efficiency of marten using a factorial MANCOVA with landscape, sex, and age as factors, and snow depth as a covariate.

We measured giving-up densities of red-backed voles from 29 May–6 June 2002. In each of two simultaneous experiments by stand, experimental food patches consisted of shallow plastic trays (30 × 25.5 cm, 8.5 cm deep) charged with a known initial mass of millet mixed uniformly in 1.5 L of medium-grain sand (4095 silica). Lids were tightly snapped onto trays for weatherproofing and to exclude birds. Entry was through 2.5-cm holes in opposite ends of the trays. Because red-backed voles are nocturnally active (Merritt 1981), we activated the trays overnight. To allow foragers to locate and acclimate to trays, we pre-baited for two days. For the following three days, we recharged and opened trays at

dusk. At dawn, we identified foragers from footprints on sooted track plates placed at entrance holes, collected the remaining millet for measurement of giving-up densities, and closed the trays. Data from trays visited by species other than red-backed voles were discarded. We dried the reclaimed millet overnight at 100°C, and weighed it to the nearest 0.01 g.

The giving-up density model assumes that foragers use a quitting-harvest rate patch-leaving rule (Brown 1988). For our first experiment, we tested this assumption by comparing giving-up densities from trays with different initial amounts of food. Equal giving-up densities recorded across trays with different initial resource levels is diagnostic of a fixed quitting-harvest rate strategy (Kotler et al. 1994). In each of 10 stands, we placed three trays, 1 m apart, under a large-diameter log. Each tray in a triplet was randomly assigned one of three initial millet densities (2, 4, or 6 g). We tested for differences in giving-up density between trays with ANOVA blocked by stand.

For our second experiment, we compared the predation risk perceived by red-backed voles between regenerating and old uncut forest. We placed the safe tray of each pair under a large-diameter log, and completely covered it with conifer boughs. We placed the corresponding risky tray 1 m away, without any cover. Ten stands in each of regenerating and uncut forests received three such pairs of trays located at the vertices of a 10-m equilateral triangle. All trays were charged with an initial millet density of 7.5 g per 1.5 L of sand. This made 45 g of millet available to foragers in each stand to control for variation in natural food abundance among stands. The value calculated for each stand was the difference in giving-up density between paired risky and safe trays, averaged over three pairs of trays per stand and three nights of measurement. Giving-up density data were log-transformed for normality.

## RESULTS

Red-backed voles ( $F_{1,26} = 2.151$ ,  $P = 0.154$ ; Fig. 1A) and meadow voles (*Microtus pennsylvanicus*) ( $F_{1,26} = 1.166$ ,  $P = 0.290$ ; Fig. 1B) did not differ significantly in abundance between regenerating and uncut forest, with red-backed voles an order of magnitude more abundant than meadow voles. Availability of subnivean access also did not differ between regenerating vs. uncut forest ( $F_{1,26} = 0.004$ ,  $P = 0.948$ ), and was unrelated to snow depth over the midwinter period, when measurements were taken ( $F_{1,24} = 0.677$ ,  $P = 0.419$ ). Marten home ranges in regenerating forest had 30% less coarse woody debris from all decay classes (1–5) combined than those in uncut forest ( $F_{1,26} = 13.147$ ,  $P = 0.001$ ; Fig. 2), and 55% less when we considered only coarse woody debris in decay classes 1–3 ( $F_{1,26} = 57.076$ ,  $P < 0.001$ ; Fig. 2).

We detected no influence of sex (Wilks' lambda = 0.690,  $F_{9,17} = 0.848$ ,  $P = 0.585$ ) or age (Wilks' lambda = 0.701,  $F_{9,17} = 0.806$ ,  $P = 0.617$ ) on hunting success by

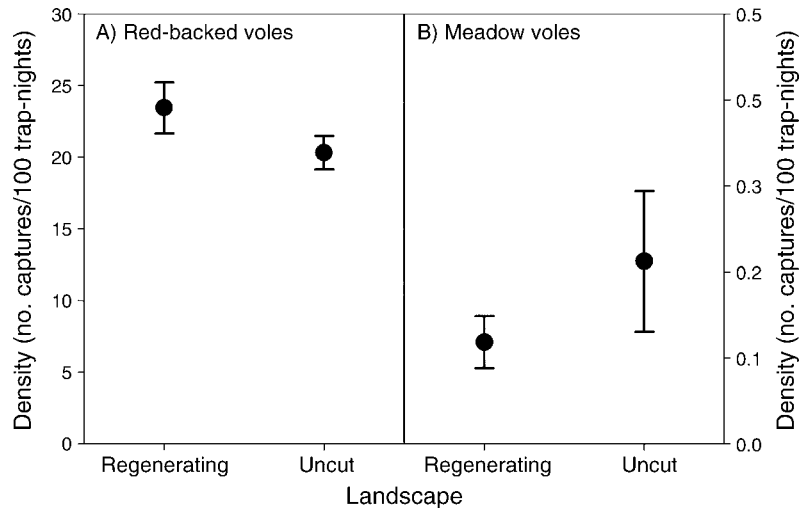


FIG. 1. Density (mean  $\pm$  SE) of (A) red-backed voles (*Clethrionomys gapperi*) and (B) meadow voles (*Microtus pennsylvanicus*) in American marten (*Microtus pennsylvanicus*) home ranges in regenerating vs. uncut forest near Ear Falls, Ontario, Canada. Small mammals were live-trapped and population density was indexed by the number of captures/100 trap-nights.

marten. Nor did we detect any significant interactions among sex, age, and landscape (sex  $\times$  landscape, Wilks' lambda = 0.633,  $F_{9,17} = 1.093$ ,  $P = 0.417$ ; age  $\times$  landscape, Wilks' lambda = 0.748,  $F_{9,17} = 0.636$ ,  $P = 0.752$ ; sex  $\times$  age, Wilks' lambda = 0.829,  $F_{9,17} = 0.390$ ,  $P = 0.923$ ; sex  $\times$  age  $\times$  landscape, Wilks' lambda = 0.852,  $F_{9,17} = 0.327$ ,  $P = 0.954$ ). Snow depth increased from 34 to 56 cm during the course of the winter, but changes in snow depth had no detectable effect on marten hunting success (Wilks' lambda = 0.489,  $F_{9,17} = 1.975$ ,  $P = 0.108$ ).

Marten hunted with less success in regenerating forest stands than in uncut forest. Encounters with small mammals per kilometer of search in regenerating forest were 42% as frequent as in uncut forest ( $F_{1,25} = 13.832$ ,  $P = 0.001$ ; Fig. 3A). Attacks on small mammals were marginally less frequent per kilometer of search in regenerating forest than in uncut forest ( $F_{1,25} = 3.744$ ,  $P = 0.064$ , Fig. 3B). Kills were 36% as frequent in regenerating vs. uncut forest ( $F_{1,25} = 6.200$ ,  $P = 0.020$ ; Fig. 3C).

Although the availability of subnivean access was similar across forest types, access points were less productive than in regenerating forest. Encounters with small mammals per access point in regenerating forest were 41% less frequent than in uncut forest ( $F_{1,25} = 20.634$ ,  $P < 0.001$ , Fig. 4A). Small-mammal attacks and kills per point were marginally less frequent in regenerating forest (attacks,  $F_{1,25} = 2.922$ ,  $P = 0.100$ , Fig. 4B; kills,  $F_{1,25} = 3.525$ ,  $P = 0.072$ , Fig. 4C).

Strike efficiency of marten on small mammals did not differ significantly between forest types (regenerating, 0.117 kills/attack, uncut, 0.147 kills/attack,  $F_{1,25} = 0.302$ ,  $P = 0.587$ ). However, because small mammals were encountered more frequently in uncut forest, their vulnerability was 1.6 times greater there than in regenerating forest ( $F_{1,25} = 6.200$ ,  $P = 0.020$ ).

There was field evidence that marten densities were higher in the uncut forest than in regenerating forest, as measured by the catch of unique individuals per 100 nights of live-trapping effort. During 2002, the marten catch per unit effort was 10.0 per 100 trap-nights in uncut stands (116 different individuals recorded over 1156 trap-nights), whereas it was 4.3 per 100 trap-nights in regenerating stands (61 different individuals caught over 1431 trap-nights). Time series analysis of the demographic data will be fully analyzed in a separate publication.

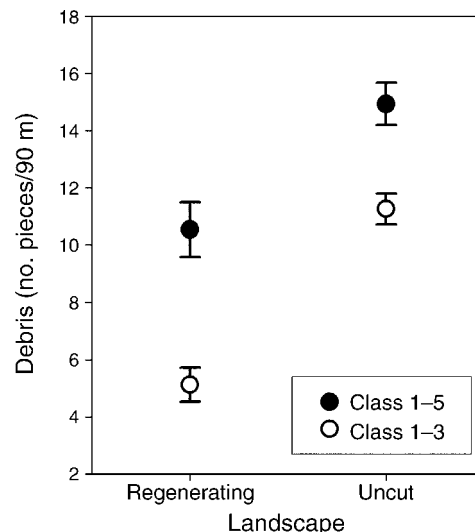


FIG. 2. Abundance (mean  $\pm$  SE) of coarse woody debris in marten home ranges in regenerating vs. uncut forest. Solid circles refer to all decay classes 1–5. Open circles refer to early decay classes 1–3. Class 1 refers to the earliest stage of decay; class 5 is the final stage of decay.

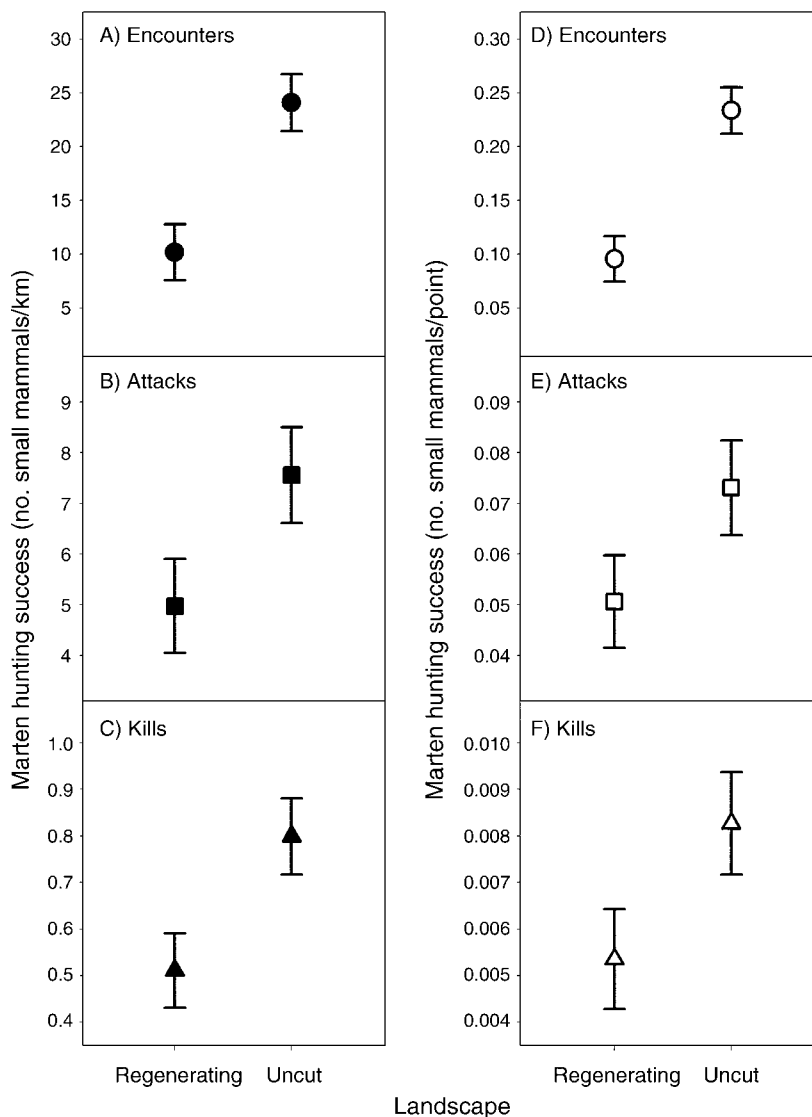


FIG. 3. Hunting success of marten in regenerating vs. uncut forest measured as the number (mean  $\pm$  SE) of small mammals that were (A) encountered, (B) attacked, (C) killed per kilometer (left-hand axis), and as the number (mean  $\pm$  SE) of small mammals that were (D) encountered, (E) attacked, and (F) killed per subnivean access point (right-hand axis).

Red-backed voles equalized giving-up densities between trays with different initial densities of millet ( $F_{2,18} = 2.850$ ,  $P = 0.084$ ), suggestive of a quitting-harvest rate strategy. The proportion of seeds consumed varied significantly with initial seed density in these trials ( $F_{2,18} = 7.381$ ,  $P = 0.005$ ), with low-density trays depleted less than intermediate or high-density trays. Both safe and risky trays were more heavily depleted in regenerating forest stands than in uncut forest stands (safe,  $F_{1,18} = 8.904$ ,  $P = 0.008$ ; risky,  $F_{1,18} = 6.019$ ,  $P = 0.025$ ). When offered paired risky and safe trays, red-backed voles always depleted safe trays more than risky trays in both forest types. The relative difference in giving-up density between paired trays was greater in uncut forest than in regenerating forest ( $F_{1,18} = 9.77$ ,  $P =$

0.006; Fig. 4), as predicted by the predation risk-sensitivity hypothesis.

#### DISCUSSION

American marten hunt small mammals by looking under logs, stumps, rocks, and in crevices (Spencer and Zielinski 1983, Thompson and Colgan 1990). In winter, marten may hunt in the subnivean space for short periods of time. Marten investigate breaks in the snow surface around structural elements, and smell or listen for prey at the upper openings of subnivean access points (Buskirk and Powell 1994, Sherburne and Bissonette 1994).

In forests, physical structure partly comes from logs, fallen trees, broken tree limbs, and stumps. These forest

structural elements are collectively called coarse woody debris. The amount and size of coarse woody debris is a function of forest age, and may be diminished by logging that removes trees before senescence. In regenerating boreal forests, the amount of coarse woody debris tends to be high following forest harvest, then declines to a minimum at  $\sim 55$  years, prior to second-growth senescence (Clark et al. 1998, Hély et al. 2000). As a result, regenerating stands 30–60 years of age tend to be structurally simpler than older stands, as demonstrated in this study and in several earlier studies (Thompson and Colgan 1987, Thompson and Curran 1995, Sturtevant and Bissonette 1997). Despite having lower levels of coarse woody debris, the availability of subnivean access in regenerating forests was not reduced, however, relative to that in old uncut forests. Additional access was created in regenerating forests by low-reaching branches of young conifer trees (Hargis and McCullough 1984), especially balsam fir and black spruce. Access points created by young conifer trees rarely contained small-mammal sign, however, and were not used by marten.

Small mammals were equally abundant during the study period in regenerating and uncut forests. This result was somewhat surprising, because several previous studies in boreal forests have found that red-backed voles are typically more common in uncut than regenerating forests (Merritt 1981, Martell 1983, Thompson and Colgan 1987, Tallmon and Mills 1994, Carey and Johnson 1995, Bellhouse and Naylor 1996, Coffin et al. 1997, Loeb 1999, Bowman et al. 2000, Butts and McComb 2000, Carey and Harrington 2001). Subsequent live-trapping studies (2002–2006) corroborated that there was little difference in small-mammal abundance between regenerating and uncut forests in our study area (J. M. Fryxell, I. D. Thompson, and J. A. Baker, *unpublished data*), so we are confident that the observed pattern during the current study was not atypical.

Structural habitat complexity enhanced, rather than diminished, the efficiency of predatory search by martens, similar to results found in several studies of predatory fish (e.g., Beukers and Jones 1998) and for some birds (e.g., Tarvin and Smith 1995). Marten did not alter hunting behavior in relation to habitat structure, but encountered, attacked, and killed fewer small mammals per kilometer of search in regenerating forests. In regenerating forests, only those subnivean access points created by coarse woody debris contained small mammals and were used by marten. These results suggest that coarse woody debris provides marten with sensory cues to the location of small mammals (Sherburne and Bissonette 1994).

There was evidence that improved hunting success by marten was linked with higher population densities in uncut vs. regenerating forest. Because we can think of no reason why hunting success should be enhanced by increased marten abundance, this correlation suggests

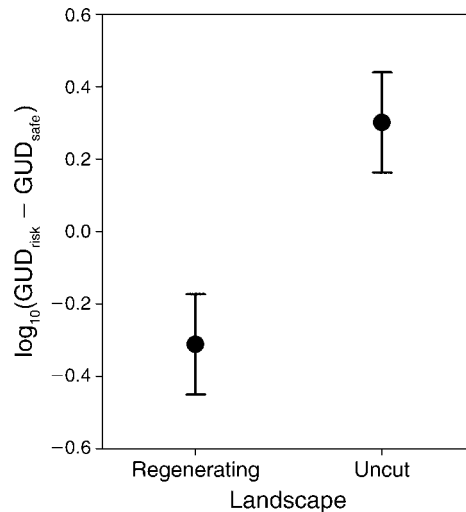


FIG. 4. Behavioral response of red-backed voles to perceived predation risk in regenerating vs. uncut forest. Response was measured as the log-transformed difference (mean  $\pm$  SE) in giving-up density (GUD) between experimental food patches in risky and safe microsites.

that martens benefited demographically from improved access to prey in uncut forests with higher degree of habitat complexity.

Red-backed voles depleted safe trays more than risky trays in all cases, indicating that they perceived a difference in predation risk, and responded by trading energy gain from risky trays for the safety of not remaining in the open. Lower giving-up densities measured from safe trays reflected the value of safety added by the brush pile placed over them. The difference in giving-up density between paired risky and safe trays was greater in uncut forest, indicating that red-backed voles perceived uncut old forests as a more dangerous habitat than the regenerating forests.

Implicit in this interpretation of our results, however, is the assumption that habitat-specific perception of predation risk by voles carries over well beyond the end of the snow-covered period when coarse woody debris improves hunting success. On the other hand, it is also possible that coarse woody debris enhances search efficiency in snow-free as well as snow-covered periods. Without further information, we cannot discriminate these alternative interpretations of the observed results. This is an intriguing topic for further behavioral study, because misplaced perception of predation risk that carries over beyond the period of true relevance would be evidence for behavioral, rather than demographically mediated, trophic response.

We believe that red-backed voles were primarily responding to marten because our track counts indicated that marten were the most common terrestrial predator. Other mustelid predators that are present in our study area, such as fisher (*Martes pennanti*) and ermine (*Mustela erminea*), also hunt small mammals in a

similar manner (Powell 1978). Other mustelids therefore probably reinforce the habitat-specific fear response by red-backed voles. Coarse woody debris provides refuge from avian predators, but not from martens. If the fear demonstrated by red-backed voles were directed primarily toward owls, then the difference in giving-up density between paired risky and safe trays should have been reversed, being greater in regenerating forest where there was both less coarse woody debris and a greater abundance of owls during the study period (D. Sleep and T. Nudds, *unpublished data*). We conclude that differential giving-up densities among red-backed voles primarily reflected fear of marten.

We have shown that although voles were equally abundant in regenerating vs. uncut forests, predation risk differed greatly as a result of habitat-mediated variation in search efficiency, due to differences in the amount of coarse woody debris. Martens were able to use this debris to better access prey below the snow surface, enhancing their hunting success. The frequency of predation events often varies among habitats (Hebblewhite et al. 2005, Hopcraft et al. 2005, Kauffman et al. 2007), so in one sense our results are not unexpected. Rarely, however, can one rule out preferential habitat use or spatial density variation by predators and/or prey as explanatory factors, rather than hunting efficiency. Recent ground-breaking work with larger carnivores that has accounted for differential habitat use suggests that hunting efficiency is influenced by proximity to riverine vegetation and erosion terraces for concealment of Serengeti lions (Hopcraft et al. 2005) and the amount of open grassland adjacent to streams for wolves (Kauffman et al. 2007). In our system, search efficiency was most affected by habitat complexity, rather than probability of successful capture once encountered.

Voles recognized and responded behaviorally to habitat-mediated vulnerability to predation. They were much more leery about using resources placed in more vulnerable areas than under cover and the degree to which predation risk-sensitivity was expressed varied across habitats, as predicted by foraging theory under dangerous conditions (see recent reviews in Bednekoff 2007, Brown and Kotler 2007). Increased wariness could potentially reduce the potential demographic impact of habitat-mediated variation in predation risk (Brown and Kotler 2007). On the other hand, if increased wariness leads to reduced food intake by voles, which is strongly suggested by our data, then behaviorally mediated changes in feeding rates could itself impose a demographic cost (McNamara and Houston 1987). Such behaviorally mediated responses have been elegantly demonstrated in bluegill sunfish in experimental ponds (Werner et al. 1983) and grasshoppers in terrestrial microcosms (Schmitz et al. 1997). The fact that similar vole densities were observed in regenerating and uncut older forest suggests that the cost of habitat-mediated predation risk is not detectable at the population level.

This is perhaps not surprising, however, given the size of marten territories, typically 2–5 km<sup>2</sup>, in our study areas. At such low population densities, martens may have little impact on vole abundance relative to other limiting factors, such as weather or variation in food supplies. Further work is needed to clarify these alternatives.

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