Test of the prey-base hypothesis to explain use of red squirrel midden sites by American martens

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Abstract: We tested the prey-base hypothesis to determine whether selection of red squirrel (*Tamiasciurus hudsonicus*) midden sites (cone caches) by American martens (*Martes americana*) for resting and denning could be attributed to greater abundance of small-mammal prey. Five years of livetrapping at 180 sampling stations in 2 drainages showed that small mammals, particularly red-backed voles (*Clethrionomys gapperi*) and shrews (*Sorex* spp.), were more abundant at midden sites than at non-midden sites. However, logistic regression indicated that middens occurred in spruce–fir (*Picea engelmannii* – *Abies lasiocarpa*) stands, being correlated with decreasing lodgepole pine (*Pinus contorta*) basal area, decreasing distance to water, and increasing canopy cover. Since middens were not randomly distributed, we constructed multiple linear regression models to determine the variability in small-mammal abundance and species richness attributable to structural and landscape variables. Regression models indicated that abundance of small mammals, red-backed voles, and uncommon small mammals could be predicted from structural and landscape variables, but midden presence did not significantly improve these models. Midden presence was a significant but weak predictor of small-mammal species richness. Our data do not support the prey-base hypothesis for explaining martens' selection of resting and denning sites near red squirrel middens at the scales we tested.

Résumé : Nous avons éprouvé une hypothèse basée sur la présence des proies pour déterminer si l'utilisation des points de cache de cônes des Écureuils roux (*Tamiasciurus hudsonicus*) comme lieux de repos et comme terriers par la Martre d'Amérique (*Martes americana*) est motivée par la plus grande abondance de petits mammifères pouvant servir de proies. Pendant 5 ans, nous avons procédé à la capture de mammifères vivants à 180 stations d'échantillonnage dans 2 bassins hydrographiques; les petits mammifères, particulièrement les Campagnols-à-dos-roux (*Clethrionomys gapperi*) et les musaraignes (*Sorex* spp.), étaient plus abondants aux points de cache qu'aux autres endroits. Cependant, une régression logistique a démontré que les points de cache se trouvaient dans des boisés d'épinettes–sapins (*Picea engelmannii* – *Abies lasiocarpa)* et étaient reliés à une diminution de la surface terrière des pins vrillés (*Pinus contorta*), à une diminution de la distance d'un point d'eau et à l'augmentation du couvert de feuillage. Parce que les caches ne sont pas réparties aléatoirement, nous avons élaboré des modèles de régression linéaire multiple pour déterminer la variabilité dans l'abondance et la richesse en espèces des petits mammifères attribuable aux variables structurales et aux variables du paysage. Les modèles ont révélé que les abondances des petits mammifères, des Campagnols-à-dos-roux et des autres petits mammifères moins communs, pouvaient être prédites par les variables structurales et les variables du paysage, mais que la présence de caches de cônes n'améliorait pas les modèles de façon significative. La présence des caches de cônes est importante, mais s'avère un mauvais indicateur de la richesse en espèces de petits mammifères. Nos résultats ne corroborent pas l'hypothèse basée sur la présence des proies pour expliquer pourquoi la martre choisit des points de cache de cônes d'écureuils comme lieux de repos et comme terriers aux échelles que nous avons utilisées.

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Introduction

Red squirrels (*Tamiasciurus hudsonicus*) are important predators of conifer seeds and are believed to have coevolved with many conifer species across North America (Smith 1970). In addition to the direct effects of feeding on conifer seeds, red squirrel feeding behavior may affect other components within forest ecosystems. Under certain conditions, red squirrels larder-hoard conifer cones by gathering hundreds of cones and caching (storing) them at specific microsites to use as a winter food supply (Hurly 1988; Hurly and Robertson 1990). Feeding activities at these larder sites result over time in vast accumulations of cone debris that are called middens (Finley 1969). Since Murie (1961), naturalists and researchers have reported the use of red squirrel middens by American martens (*Martes americana*) in western North America (Murie 1961; Buskirk 1984; Buskirk et al. 1989; Coffin 1994; Ruggiero et al. 1998; Bull and Heater 2000). Buskirk (1984) observed that 70% of marten rest sites in his south-central Alaska study occurred in red squirrel middens. Red squirrel middens were the most important variable explaining natal and maternal den site selection by martens in south-central Wyoming (Ruggiero et al. 1998). Use of middens as rest sites has also been documented in southeastern Wyoming (Buskirk et al. 1989), western Wyoming (Murie 1961), south-central Montana (Coffin 1994), western Washington (Raphael and Jones 1997), eastern Oregon (Bull and

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Heater 2000), and the northern Sierra Nevada Mountains of California (Spencer 1987; Martin and Barrett 1991). Martens may also use middens as subnivean access points (Sherburne and Bissonette 1993).

Though martens often utilize red squirrel middens, red squirrels comprise a relatively small proportion (generally <10%) of marten diets (Buskirk and Ruggiero 1994), so marten predation on red squirrels does not appear sufficient to explain their selection of middens. For example, in south-central Wyoming and south-central Alaska, where midden use is particularly strong (Buskirk 1984; Ruggiero et al. 1998), food-habit data collected concurrently with midden-use periods showed that red squirrels comprised 0% of 252 marten scats from Wyoming (L.F. Ruggiero, unpublished data) and 5.2% of 467 scats and colon contents of martens from Alaska (Buskirk and MacDonald 1984). The importance of red squirrel middens to martens for resting and denning and the limited marten predation on red squirrels prompted researchers to suggest that a symbiotic relationship may exist between these species in western North America (Buskirk 1984; Buskirk and Ruggiero 1994). This relationship between martens and red squirrels is not well understood, but is suggestive of an interaction that is more complex than a simple predator–prey interaction. That red squirrels may support marten populations through more complex interactions than simple direct predation underlines the importance of notions such as "complexity and connectedness" in the context of conservation and management of ecosystems (Christensen et al. 1996).

Two hypotheses proposed to explain marten use of middens and midden sites (areas within 15 m of middens) are (i) the thermoregulation hypothesis: martens select middens for den sites and rest sites because of their thermal properties (Buskirk et al. 1988); (ii) the prey-base hypothesis (Buskirk 1984; Buskirk and Ruggiero 1994): martens develop search images for midden sites because middens function as small-mammal aggregation points, either because small mammals use the middens directly or the middens indicate the presence of unique microhabitats, such as moist sites with large-diameter logs, that are important for small-mammal prey (see discussions in Pearson 1999). These hypotheses are not mutually exclusive. Martens may use middens for thermal cover during winter, but may also select midden areas for foraging sites in winter or during snow-free periods. Therefore, each hypothesis must be tested independently.

Buskirk et al. (1989) and Taylor and Buskirk (1994) determined that partially decayed coarse woody debris provide insulative properties that render them favorable resting and denning environments for organisms with high mass-specific thermoregulatory costs, such as the American marten. This fact, considered in conjunction with the observation that in Alaska martens often rested within middens (Buskirk 1984), which are also composed of partially decayed woody debris, supports the thermoregulation hypothesis. However, Ruggiero et al. (1998) found that martens often denned within 15 m of middens while not always denning directly within the midden as would be expected according to the thermoregulation hypothesis. Such behavior could result if middens were associated with higher numbers of small mammals, and martens preferentially selected rest sites and den sites located near higher numbers of prey.

In western North America, red squirrels often construct middens near coarse woody debris, possibly for use as feeding promontories and escape and hiding cover (Burton 1991; Smith and Mannan 1994). Middens also tend to be located within cool, wet microhabitats to prevent cones from opening as a result of desiccation (Shaw 1936; Finley 1969; Smith and Mannan 1994). Middens therefore occur in moist microsites, which tend to have large logs and decaying woody matter. Moist areas containing woody debris could favor sporocarp production by hypogeous mycorrhizal fungi (Harvey et al. 1976, 1987; Amaranthus et al. 1994), thereby attracting fungivores such as northern flying squirrels (*Glaucomys sabrinus*) and southern red-backed voles (*Clethrionomys gapperi*) (Maser et al. 1985; Maser and Maser 1988). Additionally, southern red-backed voles select logs (Nordyke and Buskirk 1991; Pearson 1994) and use soft substrates such as rotten wood and root wads for den sites (D.E. Pearson, unpublished data). Chipmunks (*Tamias* spp.), deer mice (*Peromyscus maniculatus*), and southern red-backed voles all consume conifer seeds (Abbott 1961; Schmidt and Shearer 1971; Sullivan 1979) and could be drawn to midden sites to pilfer cone caches or forage for seeds dropped by squirrels while feeding (Pearson 1999). Shrews (*Sorex* spp.) may also find middens productive sites for foraging on insects that prey on cones or are associated with the moist, woody microhabitats. Middens could therefore function to aggregate small mammals because of high densities of conifer seeds or other resources and act as sites of increased small-mammal activity. If so, martens could select these sites for feeding areas that might favor denning and resting activities nearby. For example, Zielinski (1981) found that martens often visited middens when actively foraging.

Scale plays an important role in defining ecological interactions and affecting habitat decisions made by organisms within landscapes (Wiens 1989; Ickes and Williamson 2000). This has proved true for midlevel carnivores, including American martens (Powell 1994; Oehler and Litvaitis 1996; Ruggiero et al. 1998) and their small-mammal prey (Barrett and Peles 1999; Jorgensen and Demarais 1999; Kelt et al. 1999). We therefore tested whether the prey-base hypothesis explained selection of red-squirrel midden sites by American martens at both landscape and within-stand scales by examining whether small mammals were more abundant at midden than at non-midden sites. We also examined where middens occurred within the landscape to better understand how the use of these structures by American martens relates to marten habitat selection, and we assessed the distribution of small-mammal abundance as it relates to landscape and structural variables across 2 large drainages.

Methods

The study area encompasses the Coon Creek and East Fork drainages in the Sierra Madre Range of south-central Wyoming. Elevation ranges from 2600 to 3300 m. Mean annual precipitation is about 100 cm, falling mostly as snow (70%). The snow-free period extends from mid-June to late September. The study area comprises 60% lodgepole pine (*Pinus contorta*) and 40% Engelmann spruce – subalpine fir (*Picea engelmannii – Abies lasiocarpa*) cover types.

Sampling was conducted at 180 points distributed over 2 watersheds (90 points in each) covering 24 000 ha. Points were placed

along transects at 200-m intervals, and transects were located 400 m apart. Small-mammal trapping was conducted for 5 years from 1985 to 1989 and vegetation was sampled concurrently. Structural and landscape variables and the presence or absence of middens were recorded for the area within a 15-m radius of each sampling point. Structural and landscape variables included basal area (cross-sectional surface area of the tree bole at breast height) of lodgepole pine, Engelmann spruce, and subalpine fir; canopy height; percent canopy cover; number of hard logs 20–40 cm in diameter; number of hard logs >40 cm in diameter; distance to the nearest meadow; distance to the nearest surface water; and elevation. We estimated the basal area of each tree species using a relascope. Canopy height was estimated by selecting a representative tree from the dominant and subdominant canopy layers and estimating its height in metres with a relascope. We estimated percent overstory canopy coverage by averaging concave mirror densiometer measurements taken at a distance of 5 m from the sampling point in each of the cardinal directions. Hard logs were defined as logs of decay classes 1–3 (Maser et al. 1979) ≥2 m long where ≥10% of the log was within the sampling plot. Distance to the nearest meadow, distance to the nearest surface water, and elevation were estimated from GPS locations for sampling points using GIS. In addition, we classified each site into a cover type and age-class category based on the dominance of overstory species at the sites as determined from estimates of basal area and diameter at breast height (DBH) as follows: L8 = lodgepole pine 6–22 cm DBH; L9 = lodgepole pine 23–35 cm DBH; S8 = spruce–fir 6–22 cm DBH; S9 = spruce–fir 23–35 cm DBH; or wet meadow. We defined middens as red squirrel feeding sites where cone debris was ≥1 m in diameter at the widest point.

We trapped each sampling point for small mammals once per year by centering 6 trap stations in a rectangular grid (2 by 3 stations at 15-m spacing) on the center point. One pitfall (approximately 23 cm wide by 24 cm deep) and 2 Sherman live traps were placed at each trap station. Pitfall traps were opened for 9 days and live traps were set for 8 days during each sampling period. Live traps were baited with peanut butter and rolled oats. Trap-nights totaled 150 per sampling station per year for the two trap types combined. Small mammals were toe-clipped in a generic manner to determine recapture status (i.e., whether they had been previously captured or not), but unique numbers were not assigned to each animal. Traps were checked once each morning and animals were identified to species and their age, sex, mass, and reproductive status were determined before release. Dead animals were collected and species identifications were confirmed on the basis of dental characteristics. Common and scientific names used herein follow Jones et al. (1997). Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

We used multiple logistic regression to determine the relationship between landscape and structural variables and the distribution of middens in the landscape. We then used multiple linear regression to statistically control for structural and landscape variables that might cause spurious correlations between midden presence and small-mammal abundance or species richness. Using backward stepwise regression, we developed statistical models that maximized our understanding (r^2 adjusted) of the relationship between the independent predictive variables and abundance of small mammals, abundance of red-backed voles, abundance of uncommon species (defined as all species other than red-backed voles and deer mice (Table 1) to account for the collective group of small mammals minus these two dominant species), and species richness (defined as the total number of small-mammal species captured at each sampling station). We then added midden presence to each model as an independent variable to determine whether knowledge

of the presence or absence of a midden made a significant contribution to the regression model. Forward and backward stepwise regressions were also conducted with middens entered first and last and showed no evidence that entry position affected the model results. We also tested univariate linear regression models using only midden presence as an independent variable to determine its ability to predict small-mammal abundance in the absence of structural and landscape variables. One-way ANOVA was used to compare average numbers of small mammals captured at midden versus non-midden sites. We transformed data where necessary using natural logarithm and square-root transformations to meet regression assumptions (SPSS Inc. 1994). We used indices of small-mammal abundance (number of unique individuals captured) because sample sizes were too small for effective model selection necessary for conducting mark–recapture population estimates, a condition that results in poor population estimation using mark–recapture models (Menkins and Anderson 1988; McKelvey and Pearson, unpublished data[2]).

Results

Trapping effort over the 5-year study period for the 180 sampling points resulted in 91 800 trap-nights that produced 8457 individuals and 14 species of small mammals. Red-backed voles dominated the captures, followed by deer mice, cinereus shrews (*Sorex cinereus*), montane shrews (*Sorex monticolus*), Uinta chipmunks (*Tamias umbrinus*), least chipmunks (*Tamias minimus*), and other, less common small mammals (Table 1). Red squirrel middens occurred at 20 (11%) of the 180 sampling points. ANOVA results indicate that average numbers of individuals captured were significantly higher at midden than at non-midden sites for 3 of 14 species: red-backed voles ($F_{[1,178]} = 15.45$, $P < 0.001$), montane voles ($F_{[1,178]} = 4.35$, $P = 0.038$), and cinereus shrews ($F_{[1,178]} = 10.26$, $P = 0.002$) (Table 1). This difference was especially pronounced for red-backed voles and cinereus shrews, which were nearly twice as abundant at midden sites than at non-midden sites.

However, midden presence at a site was strongly negatively correlated with lodgepole pine basal area (Wald statistic, $\chi^2 = 16.867$, $P < 0.001$) and elevation (Wald statistic, $\chi^2 = 10.003$, $P = 0.002$) and positively correlated with increasing canopy cover (Wald statistic, $\chi^2 = 4.76$, $P = 0.029$) based on multiple logistic regression analysis ($\chi^2_{[3]} = 44.28$, $P < 0.001$). Overall classification success for the model was 91.1%. In general, red squirrels constructed middens in mature and old-growth spruce–fir stands and avoided using lodgepole pine or young spruce–fir stands. Seventeen of the 20 middens observed (85%) occurred in the S9 cover type. Because middens were not randomly distributed within the study area and were in fact negatively correlated with the occurrence of lodgepole pine, which red-backed voles (the most common species captured) are also known to avoid (Nordyke and Buskirk 1991; Pearson 1994, 1999), we felt that it was necessary to statistically control for structural and landscape variables using multiple regression.

Structural and landscape variables were significant for abundance of all species combined ($P < 0.001$), red-backed voles ($P < 0.001$), and uncommon species ($P < 0.001$) and for species richness ($P < 0.001$) (Table 2). Increasing canopy height

[2]K.S. McKelvey and D.E. Pearson. Population estimation with sparse data: the role of indices versus estimators revisited. Submitted for publication.

Table 1. Total numbers of individuals captured and numbers (mean ± standard error) captured at midden and non-midden sites for 14 species of small mammals.

	Total no. of individuals captured	No. captured at non-midden sites ($n = 160$)	No. captured at midden sites ($n = 20$)
*Clethrionomys gapperi**	4468	22.74 ± 1.46	41.45 ± 6.80
Microtus longicaudus	22	0.13 ± 0.03	0.05 ± 0.05
*Microtus montanus**	93	0.43 ± 0.11	1.25 ± 0.66
Peromyscus maniculatus	1823	10.15 ± 0.78	9.95 ± 1.61
Phenocomys intermedius	76	0.42 ± 0.05	0.45 ± 0.15
*Sorex cinereus**	893	4.57 ± 0.37	8.10 ± 1.07
Sorex hoyi	12	0.06 ± 0.02	0.10 ± 0.07
Sorex monticolus	393	2.08 ± 0.36	3.05 ± 0.83
Sorex nanus	2	0.01 ± 0.01	0.00 ± 0.00
Sorex palustris	13	0.07 ± 0.03	0.10 ± 0.07
Spermophilus lateralis	35	0.21 ± 0.08	0.10 ± 0.10
Tamias minimus	173	0.89 ± 0.17	1.55 ± 0.80
Tamias umbrinus	322	1.84 ± 0.30	1.35 ± 0.44
Zapus princeps	132	0.69 ± 0.12	1.10 ± 0.56

*Significant difference at the $\alpha = 0.05$ level.

Table 2. Contribution of the midden-presence variable to multiple linear regression models that use structural and landscape variables to predict the number of small mammals, number of red-backed voles, number of individuals of uncommon species, and species richness at each of 180 sampling points.

Regression results for:	Independent variable	Dependent variable			
		No. of individuals of all small-mammal species	No. of red-backed voles	No. of individuals of uncommon species	Species richness
models based on structural and landscape variables	Canopy cover		2.41	–3.00	
	Canopy height	3.45		4.01	2.91
	Elevation	–3.22	–4.22		
	Distance to water	–2.81			–2.17
	Distance to meadow			–2.42	–2.02
	Lodgepole pine basal area	–6.87	–2.98	–3.50	
	Spruce basal area		3.87		
	Subalpine fir basal area		3.32		
	No. of hard logs 20–40 cm diameter				
	No. of hard logs >40 cm diameter		3.53		
	F	36.221	34.901	19.683	8.346
	P	<0.001	<0.001	<0.001	<0.001
	r^2	0.453	0.548	0.310	0.125
models with midden variable added	*P*	0.599	0.286	0.219	0.033
	r^2	0.454	0.551	0.316	0.147
univariate models	*P*	<0.001	<0.001	0.005	0.005
	r^2	0.076	0.065	0.044	0.044

Note: The *t* scores are given for variables significant at $\alpha = 0.05$. Stepwise multiple regression was used to generate landscape- and structural-variable models. The midden variable was then added to determine its contribution to these models using multiple linear regression. The r^2 values after adding the midden variable indicate the new overall r^2, and *P* values indicate the improvement of the model with the midden variable added over the landscape and structural variable model (models with midden variable added). Univariate models show the contribution of the midden variable independently of all other variables.

and decreasing elevation, distance to water, and lodgepole pine basal area together explained 45% of the variability in the total number of individuals captured for all species combined ($r^2 = 0.453$). Addition of the midden-presence variable to this model did not significantly improve it ($P = 0.599$, $r^2 = 0.454$), and midden presence explained little variation in number of animals in univariate regression ($r^2 = 0.076$). Abundance of red-backed voles at a site was effectively

Table 3. Total numbers of individuals captured and numbers (mean ± standard error) captured at midden and non-midden sites within S9 (mature and old-growth spruce–fir) habitat for 14 species of small mammals.

	Total no. of individuals captured	No. captured at non-midden sites ($n = 46$)	No. captured at midden sites ($n = 17$)
Clethrionomys gapperi	2402	35.37 ± 3.49	45.59 ± 7.52
Microtus longicaudus	13	0.26 ± 0.10	0.06 ± 0.06
Microtus montanus	35	0.30 ± 0.09	1.24 ± 0.75
Peromyscus maniculatus	465	6.76 ± 0.87	9.06 ± 1.77
Phenocomys intermedius	30	0.50 ± 0.11	0.41 ± 0.15
Sorex cinereus	426	6.20 ± 0.72	8.29 ± 1.18
Sorex hoyi	6	0.09 ± 0.05	0.12 ± 0.08
Sorex monticolus	165	2.50 ± 0.55	2.94 ± 0.86
Sorex nanus	1	0.02 ± 0.02	0.00 ± 0.00
Sorex palustris	9	0.15 ± 0.09	0.12 ± 0.08
Spermophilus lateralis	2	0.00 ± 0.00	0.12 ± 0.12
Tamias minimus	40	0.59 ± 0.24	0.76 ± 0.43
Tamias umbrinus	91	1.48 ± 0.44	1.35 ± 0.51
Zapus princeps	51	0.85 ± 0.35	0.71 ± 0.36

Note: None of the means differ at the $\alpha = 0.05$ level.

predicted by higher canopy cover, lower elevation, lower lodgepole pine basal area, and increased sprucefir basal areas ($r^2 = 0.548$). Adding midden presence to this model did not improve it significantly ($P = 0.286$, $r^2 = 0.551$), nor did midden presence explain much variation in number of red-backed voles in univariate regression ($r^2 = 0.065$). The abundance of uncommon species was best predicted by lower percent canopy cover, greater canopy height, shorter distance to meadows, and lower lodgepole pine basal area, but these variables provided only poor to moderate predictive capability ($r^2 = 0.310$). Midden presence added very little to the predictive capability of this model ($P = 0.219$, $r^2 = 0.316$), and midden presence explained only 4% of the variability in abundance of uncommon small mammals captured in the study area using univariate regression ($r^2 = 0.044$). Comparisons of small-mammal captures for only the sampling stations occurring within the S9 cover type indicate that the differences in small-mammal abundance between midden and non-midden sites are greatly reduced once the data are stratified by this landscape variable. None of the differences are significant at the $\alpha = 0.05$ level (Table 3). Species richness was weakly predicted by increased canopy height and decreasing distance to meadow and water ($r^2 = 0.125$). The presence of a midden at the trap site significantly improved the ability of a regression model to predict an increase in species richness ($P = 0.033$); however, the improved model was still weak ($r^2 = 0.147$) and midden presence explained very little variation in species richness in univariate regression ($r^2 = 0.044$).

Discussion

Buskirk et al. (1989) and Taylor and Buskirk (1994) examined the efficacy of the thermoregulatory hypothesis as a proximal mechanism for marten selection of midden sites by examining the thermal properties of decayed woody materials and other potential den structures. Their work showed that decayed woody debris provided superior thermal properties compared with ambient conditions and conditions at other available den sites such as rock dens and snag cavities. Given the insulative properties of woody material such as that found in middens, winter use of middens as rest sites in western North America (Buskirk 1984; Spencer 1987; Martin and Barrett 1991; Coffin 1994; Raphael and Jones 1997; Bull and Heater 2000) supports the thermoregulation hypothesis. However, Ruggiero et al. (1998) found that although middens were the most important variable affecting den-site selection, the actual den structure was often adjacent to rather than directly within the midden. Their data suggest that selection of midden sites by American martens may also be affected by factors other than the insulative properties of middens.

In testing the prey-base hypothesis of marten selection of red squirrel midden sites, we found that small mammals were more abundant at midden sites than at non-midden sites across the landscape as indicated by comparisons of captures by species and simple linear regression results (Tables 1, 2). These data suggest that at the coarsest scale, the presence of red squirrel middens and small-mammal abundance are strongly correlated. However, middens occurred almost exclusively in mature and old-growth spruce–fir stands, where small mammals were relatively abundant whether a midden was present or not. As a result, variation in small-mammal abundance was better explained by landscape features such as tree basal area that defined cover type and within-stand features such as coarse woody debris than by the presence or absence of middens. Since middens are a within-stand feature, it seems unlikely that martens use them to determine the landscape-level distribution of small mammals. Once within a stand, martens could use middens to locate small-mammal hot spots if small mammals were more abundant at midden sites than at other sites within the stand. However, our results indicate that small mammals were not significantly more abundant at midden sites than at non-

midden sites within older spruce–fir stands and that other structural features were better suited to predict small-mammal abundance than middens. These results suggest that it is not middens, but other structural features with which middens are associated, such as coarse woody debris, that drive the distribution patterns of small-mammal abundance in this area.

Since red squirrels were observed at all 180 sampling stations during point counts conducted concurrently with this study (L.F. Ruggiero, unpublished data), we reason that the predominance of middens within spruce–fir stands resulted not from red squirrels' avoidance of lodgepole pine but from behavioral decisions made by red squirrels regarding cone-caching strategies. Squirrels in the study area larder-hoarded within spruce–fir stands, producing well-developed middens, while the lack of middens in lodgepole pine stands suggests that squirrels mostly scatter-hoarded in these areas. Others have reported "small middens" in lodgepole pine stands that may have resulted from scatter-hoarding behavior (Hatt 1943; Finley 1969; Gurnell 1984). Although larder-hoarding occurs in lodgepole pine (Gurnell 1984), scatter-hoarding may be the general trend within this cover type, possibly because small seeds, fewer seeds per cone, and fewer cones per tree render many lodgepole pine stands suboptimal foraging habitat for red squirrels (Finley 1969; Smith 1970, Rusch and Reeder 1978; Hurly and Robertson 1990). Though scatter-hoarding is recognized as an alternative strategy to larder-hoarding for red squirrels in eastern deciduous forests and some pine plantations and forests (Layne 1954; Hurly and Robertson 1990; Burton 1991), we found no studies comparing red squirrels' caching strategies among forest cover types in western North America. Understanding where middens occur in the landscape is useful in light of their importance as habitat features for American martens and other forest carnivores.

Examining the small-mammal data from the standpoint of marten habitat use and diet is informative. In the Rocky Mountains, martens tend to favor mature and older stands composed of moist cover types such as spruce and fir (see Buskirk and Ruggiero 1994). Red-backed voles generally dominate marten diets (Buskirk and Ruggiero 1994; Bull 2000), but reportedly occur in proportion to their availability in studies where small-mammal sampling has been conducted in conjunction with marten diet studies (Weckwerth and Hawley 1962; Buskirk and McDonald 1984). This is not surprising, given that red-backed voles exhibit habitat selection very similar to that of martens in the Rocky Mountain Region (Raphael 1988; Nordyke and Buskirk 1991; Pearson 1999; Hayward and Hayward 1995). Our data, which are the first, to our knowledge, to present habitat associations of red-backed voles on such a large scale (24 000 ha covering 2 drainages), suggest that red-backed voles favored spruce–fir stands over lodgepole pine as their numbers increased with increasing spruce and subalpine fir basal area and decreasing lodgepole pine basal area. Other studies comparing lodgepole pine with other cover types in the Rocky Mountains have shown that red-backed voles avoid some lodgepole pine stands (Pearson 1994; Hayward and Hayward 1995), whereas

other cover types may function as sink habitats (Nordyke and Buskirk 1991).

The landscape perspective of this study provides new information about the effect of elevation on red-backed voles in western North America, which is not reported in site-specific small-mammal studies. The negative coefficient for elevation was the strongest in the regression model of red-backed vole abundance. This relationship is probably partly due to a correlation between elevation and cover type, with spruce being generally at lower elevation than lodgepole pine in the Coon Creek – East Fork study area, but it is also likely attributable to higher productivity found at lower elevations, given the high elevation of the study area. Greater canopy cover associated with increasing red-backed vole abundance may be attributed partly to the association with spruce–fir cover types and partly to greater site productivity. Since distance to water was not an important variable, it is reasonable to conclude that the elevation relationship was not simply a function of red-backed voles being in drainage bottoms, where spruce often occurs. The association between southern red-backed voles and large-diameter logs has been reported in other Rocky Mountain studies (Nordyke and Buskirk 1991; Pearson 1994).

Dietary studies have also shown that *Microtus* spp. are important prey for martens in western North America (Buskirk and Ruggiero 1994). Although *Microtus* spp. generally comprise a smaller proportion of the total diet of martens, they often occur in marten diets in higher proportions than expected based on availability (Weckwerth and Hawley 1962; Douglass et al. 1983; Buskirk and MacDonald 1984). This is particularly interesting, given that *Microtus* spp. tend to be associated with open grass and forb habitats (Hayward and Hayward 1995; Pearson 1999), which martens are thought to avoid in winter (Lensink 1953; Hawley and Newby 1957; O'Doherty et al., submitted for publication[3]). However, within forest habitats, *Microtus* spp. often occur in grass and forb microsites near wet areas such as streams or in light gaps and other openings that favor their habits (Buskirk and McDonald 1984; Pearson 1999). Given the habitat specificity of *Microtus* spp. within forest habitats and the selection of *Microtus* spp. exhibited by martens, it seems likely that martens seek out such microhabitats to forage for *Microtus* spp. or use edges of meadows and other open habitats (Weckwerth and Hawley 1962; Spencer and Zielinski 1983; Buskirk and McDonald 1984; Pearson 1999).

That midden sites exhibited greater species richness than non-midden sites even after landscape and structural variables were statistically controlled for suggests that middens are associated with greater habitat heterogeneity within a given set of structural and landscape conditions. Midden sites supported not only forest species such as red-backed voles and cinereus shrews that might be expected to occur at middens, given the greater canopy cover observed at these sites, but also favored species generally associated with more open grass, forb, and shrub habitats, such as montane voles (*Microtus montanus*), western jumping mice (*Zapus princeps*), and least chipmunks (Clark 1973; Cranford 1983; Clark and

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[3] E.C. O'Doherty, L.F. Ruggiero, and M.G. Raphael. Winter responses of American martens to small clearcuts in Wyoming. Submitted for publication.

Stromberg 1987; Raphael 1988; Pearson 1999). The presence of such species at midden sites suggests that middens may be associated with microhabitats such as light gaps in the canopy or natural forest openings not detected by our sampling methods because they may have occurred at a different scale.

Our data indicate that at the landscape scale middens are correlated with greater abundance of small mammals, but it is unlikely that martens are using the presence of middens to make habitat-selection decisions at this scale. After landscape and structural variables were accounted for, middens contributed little information to regression models of small-mammal abundance. We therefore conclude that our data do not support the prey-base hypothesis as an explanation for marten selection of midden sites at the scales we examined. However, we caution that our data address the prey-base hypothesis at the landscape scale and at a coarse-grained, within-stand scale because our small-mammal trapping areas were large (15×30 m) relative to the actual midden structures (mean diameter 3.0 m), so the trapping area was relatively loosely tied to the midden itself and reflects small-mammal abundance and activity in the vicinity of the midden, i.e., the midden site. Moreover, midden sites did continue to show somewhat more red-backed voles and montane voles than non-midden sites even within mature and old-growth spruce–fir stands, though this relationship was not significant. More detailed studies within spruce–fir habitat that focus on microhabitat use by small mammals where trapping is directed at the midden itself rather than a general area containing a midden would be necessary to effectively test the prey-base hypothesis at a finer scale. Moreover, prey abundance is not the only factor that can effect a predation response. Prey vulnerability can be more important than prey abundance for predator success. We did not test for differential prey vulnerability between midden and non-midden sites. We also did not assess the potential influence of midden size or number on small-mammal abundance, as we treated middens as binary variables. That small-mammal diversity was significantly correlated with midden presence suggests that the prey-base hypothesis should be tested at finer resolution at the microhabitat scale.

The American marten is an important forest carnivore used in many national forests as a management indicator species for old-growth conditions (Buskirk and Ruggiero 1994). Critical life-history behaviors of martens such as denning and resting have been closely linked not only to forest-generated structural components such as snags and coarse woody debris, but also to a wildlife-generated structural component, the red squirrel midden. Although one important attribute of the red squirrel midden, its thermal properties, has been established, the link between martens and red squirrel middens appears to be more complex. At the landscape scale, red squirrel middens correlated with greater small-mammal abundance, but it seems more likely that martens make habitat choices at the landscape scale on the basis of such features as cover type and structural attributes which may more directly reflect the availability of food and denning and resting habitat than the prevalence of middens. We also found insufficient evidence to support the prey-base hypothesis at the within-stand scale. However, at the microhabitat scale, the importance of midden sites for denning and resting is well established and the correlation between middens and small-mammal species richness observed here suggests that the prey-base hypothesis should be more carefully examined at this scale as a potential explanation for selection of red squirrel midden sites by American martens.

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