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MARTEN SUBNIVEAN ACCESS POINT USE: RESPONSE TO SUBNIVEAN PREY LEVELS

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Abstract: Because marten (*Martes americana*) require subnivean access for cover, prey access, and homeothermic reasons, we developed a predictive model to explain their differential use of subnivean access holes in Yellowstone National Park. We included prey biomass and percent ground cover of coarse woody debris (CWD) as explanatory variables in a logistic regression model because of their biological importance to marten in winter. Taken singly, relative prey biomass yielded the best univariate predictive model (P = 0.001). However, we included CWD in a multivariate model because of its biological significance. Coarse woody debris provides structure that intercepts snowfall, creating subnivean tunnels, interstitial spaces, and access holes, and was found at used and unused access points. Mean prey biomass was 205.4 g/400 m^2 (SE = 20.26) and 109.2 g/400 m^2 (SE = 10.73) at used and unused points ($P < 0.001$), respectively, while mean percent ground cover of CWD was 24.7 (SE = 2.30) and 18.5% (SE = 1.18) at used and unused access points ($P = 0.017$), respectively. As CWD increased by 5%, the probability of use by marten increased 1.12 times, and for every 50 g increase in relative prey biomass, marten were 1.37 times more likely to use that access point. Prey biomass varied ($P < 0.001$) among subnivean access points, and marten chose between different access points primarily on the basis of prey abundance levels. Older growth forests with accumulated CWD will enable marten to forage effectively in winter.

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Key words: marten, *Martes americana*, predation, prey, subnivean access, Wyoming.

In winter, marten require subnivean access (Pulliainen 1981, Buskirk 1984, Buskirk et al. 1989), but the mechanisms that determine use of some access points over others are unclear. Food availability, escape cover, and homeothermic requirements have been hypothesized as important factors affecting use of subnivean access points. There also is a relationship between use of access points and the presence of CWD. Coarse woody debris breaks the snow surface and provides access to the subnivean zone. Buskirk et al. (1989) found that 49% of marten resting sites and 63% of resting episodes were associated with CWD. Corn and Raphael (1991) reported higher CWD levels at used access points than at randomly sampled points. Buskirk et al. (1989) suggested that marten used subnivean access points primarily to reach CWD that provides thermal insulation. Marten in Wyoming (Buskirk et al. 1989) used access sites associated with CWD when ambient temperatures were coldest. Buskirk et al. (1988) reported that a mean depression in body temperature of 2.9 C produced an estimated energy savings of 4%. Taylor (1993), and Taylor and Buskirk (Univ. Wyoming, Laramie, unpubl. data) reported that subnivean cavities associated with CWD offered a warmer microenvironment when convective losses were high outside the cavity. The energy savings associated with resting in subnivean spaces instead of above the snow was approximately 23% (S. W. Buskirk, Univ. Wyoming, Laramie, pers. commun.). Studies of marten temporal activity patterns, however, have shown that they were most active at night during winter (Lensink et al. 1955, Zielinski 1981, Zielinski et al. 1983) when temperatures were coldest. These observations imply that other mechanisms may contribute to access point use.

Marten and other mustelids have metabolic rates that are 20–>100% higher than those of other mammals with similar body size (Brown and Lasiewski 1972, Iversen 1972, Casey and Casey 1979, Korhonen et al. 1983). Brown and Lasiewski (1972) attributed the increased basal metabolic rate of weasels (*Mustela frenata*) to their elongated body shape, which, combined with relatively thin and poorly insulative fur (Casey and Casey 1979), sacrificed energetic ef-

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Our objective was to identify variables that influenced subnivean access by marten, specifically the relationship between location of subnivean access and relative prey abundance. We also attempted to determine the role of CWD in marten's choice of snow tunnels. We tested the hypotheses that differential use of access points by marten was positively correlated with clumped subnivean prey and access point use was positively correlated with percent cover of CWD.

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STUDY AREA

We chose the Canyon-Norris region of Yellowstone National Park as a study area because it contained a variety of marten habitats and provided a road network for telemetry and access to marten habitat by foot. The major habitat was dominated by lodgepole pine (*Pinus contorta*) with small- to moderately sized spruce-fir inclusions. During summer 1988, varying degrees of fire intensity created a mosaic of burned, partially burned, and unburned habitats. Elevation ranged from 2,500 to 3,500 m. Temperatures ranged from 5 to −60 C in winter and from 25 to −5 C in summer. Normal snow accumulation during winter was about 2 m (Yellowstone Natl. Park, unpubl. data).

METHODS

Access Point Sampling

We sampled and compared used and unused access points within marten home ranges. We defined an access point as any opening through the snow surface to the subnivean zone. At each used and unused access point, we described habitat and made 4 habitat measurements (canopy cover density, percent ground cover, percent dead and downed CWD, and snow depth [cm]) at 4 randomly selected locations in a 5-m-radius plot centered on each access point. We measured mean canopy cover density with a convex densiometer. Percent ground cover and CWD were estimated in 10% increments. We measured snow depth with a meter stick. We measured relative prey abundance in a 25-m^2 plot centered on each access point (Sherburne 1992).

During winters 1990 and 1991, we determined access point use by tracking marten in the snow. We trapped 22 marten and fitted them with 40-g radio transmitters. We relocated each marten in a random sequence throughout winter and then skied into the area and backtracked the animal until we located 10 used access points or lost the tracks. Each used access point was paired with the first unused point we found within 25 m of the used site. We judged access points to be unused if there was no evidence of tracks or other disturbance in the snow. These access points could have been used later, although incidental checks of 20 unused points subsequently showed this was rare. We used a stratified random sampling method to avoid sampling areas that did not represent marten habitat (i.e., meadows within home ranges).

Small Mammal Sampling

We trapped small mammals during summer at the exact sites where used and unused winter access points were identified. Snow cover prohibited small mammal trapping in the winter, so trapping occurred immediately after the ground became accessible. We randomly selected 70 used and 74 unused sites. Sites closer than 100 m to each other were not sampled to avoid sampling the same subpopulations. Al-

Table 1. Number of subnivean access points used by marten in response to different levels of prey biomass and coarse woody debris in Yellowstone National Park, Wyoming, 1989–91.

Variable	Subnivean access points		
	Used	Unused	Total
Relative prey biomass (g/25 m^2)			
Low (0–90)	22 (32.1)[a]	44 (33.9)	66
Intermediate (91–180)	16 (16.5)	18 (17.5)	34
High (>180)	32 (21.4)	12 (22.6)	44
Total	70	74	144
Coarse woody debris (%)			
Low (0–33)	22 (23.3)	26 (24.7)	48
Intermediate (34–66)	32 (36.5)	43 (38.5)	75
High (>67)	16 (10.2)	5 (10.8)	21
Total	70	74	144

[a] Observed (expected) values.

though their home ranges are smaller during winter, microtines do not tend to relocate during summer (Cranford 1984, Herman 1984, Madison 1984). We expected that microtine population levels would vary during summer; however, we attempted to keep the bias constant across all sites by sampling prey at all points within a 3-week period. To test the assumption that winter prey levels at access points were similar to summer prey levels, we prepared boluses composed of seeds in a paraffin matrix and placed these in access holes. Our results showed a relationship between winter bolus use and summer abundance index (Sherburne 1992). We placed snap traps 5 m apart in a grid of 25 stations, centered on used and unused access points. We trapped for 3 days and recorded the number of small mammals captured. We identified prey by species to allow calculations of relative prey biomass on the basis of average mass of individuals within a species. We used the relative prey abundance index at access points to determine relative biomass as an indicator of overall food value available to marten at each point.

Analyses

We used a Student's *t*-test to compare differences in canopy cover, percent ground cover, snow depth, relative prey biomass, and CWD between used and unused access points. We used multivariate analysis techniques to identify relations between measured variables and access point use. Categorical interdependence methods, including G^2 analysis and logistic regression (Hosmer and Lemeshow 1989) were used to determine if dependency relationships existed between access point use, relative prey biomass, and CWD. We characterized results of the logistic regression with the Wald test statistic ($W = \hat{B}_1/\mathrm{SE}\,[\hat{B}_1]$), which was obtained by comparing the maximum likelihood estimate of the slope parameter ($\hat{B}_1$) to an estimate of its standard error, under the hypothesis that $\hat{B}_1 = 0$ follows a standard normal distribution. Hence, the critical value was 1.96. We transformed relative prey biomass using a square-root function prior to analysis. We calculated cross product (odds) ratios (Agresti 1984) for relative prey biomass and CWD to describe the strength of the association and allow a direct interpretation of the influence of each variable upon access point use.

RESULTS

Mean prey biomass was 205.4 g/400 m^2 (SE = 20.26) and 108.2 g/400 m^2 (SE = 10.73) at used and unused points ($t = 4.24$, 105 df, $P < 0.001$), respectively, while mean percent ground cover of CWD was 24.7 (SE = 2.30) and 18.5% (SE = 1.18) at used and unused access points ($t = 2.39$, 103 df, $P = 0.017$), respectively. When relative prey biomass and CWD levels at each access point were classed into low, intermediate, and high levels, we found that use of subnivean access points by marten was associated ($P < 0.001$) with high prey biomass and to a lesser extent ($P < 0.025$) with increasing CWD (Table 1).

Univariate logistic regression indicated that relative prey biomass was a good predictor of differential access point use ($W = 3.96$, $P < 0.001$). Coarse woody debris was an adequate predictor of differential access point use ($W = 2.32$, $P = 0.023$). The fit of a multivariate model, created using access point use as the response variable and CWD and relative prey biomass as explanatory variables (Fig. 1), was adequate ($P = 0.216$) with relative prey biomass showing good predictive power ($W = 3.74$, $P < 0.001$). Coarse woody debris was not significant in the multivariate model ($W = 1.81$, $P = 0.072$). Log odds ratios showed that marten were 1.37 times more likely to use an access point with every 50 g increase in biomass and 1.12 times more likely for every 5% increase in CWD. Canopy cover, percent ground cover, and snow depth were not related ($P > 0.05$) to access point use.

DISCUSSION

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gression models explaining use of subnivean access points by marten. Coarse woody debris provided marten with access to the subnivean zone. Buskirk (1984) and Buskirk et al. (1989) noted that CWD may provide thermal benefits. Their data suggested a threshold temperature effect may exist. As temperatures decrease marten appear to use access points more frequently for thermal advantage. As a consequence, total time spent active should decrease. Indeed, in more northerly and colder climates, marten appeared to increase activity during warmer seasons (Zielinski 1981, Buskirk 1983). Bissonette et al. (1988), Fredrickson (1990), and G. S. Drew (Natl. Biol. Surv., pers. commun.) documented periods of apparent total inactivity by marten at times of very cold temperatures (< −25 C).

Use of access points also could be influenced by predators. Mammalian and avian predators kill marten. In Newfoundland, marten responded to terrestrial predators by climbing trees (Bissonette, unpubl. data). Most raptors migrated south of Newfoundland in winter, leaving 4 owl species (great horned [*Bubo virginianus*], boreal [*Aegolius funereus*], snowy [*Nyctea scandiaca*], and northern hawk-owl [*Surnia ulula*]) (Bull and Farrand 1977) as primary avian predators. We believe marten responded to owl predation by using subnivean cover; however, we do not have data to support this hypothesis. Choice of habitat (i.e., forest, meadows, clear-cuts), however, was influenced by predators (Drew and Bissonette, unpubl. data).

In our study area, CWD was abundant and widespread, and potential subnivean access points were abundant. Marten bypassed a number of potentially available subnivean access points before using a seemingly similar point. When used and unused points were compared, relative prey biomass and CWD were the only variables that differed. Canopy cover, percent ground cover, and snow depth were not related to access point use. Prey biomass consistently showed a stronger relationship to access point use than CWD. While CWD provided access to prey by providing structure that intercepted snow fall, thus creating passages, it was the presence of prey that dictated differential access point use by marten. We found no relationship between relative prey biomass and CWD levels. Marten appeared to be able to discriminate between access points with high prey levels and those with low prey levels.

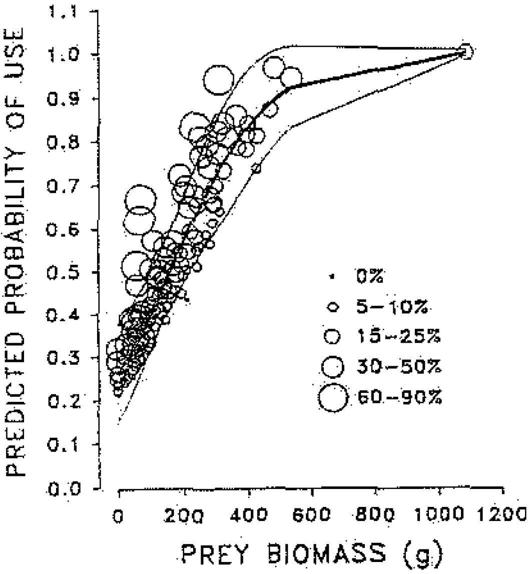

Fig. 1. Probability of access point use by marten in Yellowstone National Park, 1989–91, as a function of prey biomass (g) and coarse woody debris (% cover). Area of open circles is proportional to coarse woody debris level. The dark solid line describes the relationship between prey biomass found at subnivean access holes and the predicted probability of use of the access point by marten. The lighter solid lines represent 95% confidence intervals.

The pattern of marten choice of access points on the basis of prey abundance appears clear. However, we do not yet understand how marten make their selection. At least 2 possible mechanistic explanations appear worth investigating. Marten may use either auditory or olfactory cues to assess presence of small mammals in subnivean locations. Some voles may group together during winter (Cranford 1984) providing stronger olfactory cues than if they existed solitarily. Similarly, voles or other small mammals in groups may emit a higher frequency and volume of auditory cues than do single conspecifics. Field and laboratory experiments are needed to explain how marten are able to distinguish between access points with higher subnivean prey levels.

MANAGEMENT IMPLICATIONS

The world's coniferous forests, the source of most industrial wood production, covered 1.1 billion ha or 27% of the world's total forest area in 1985 (Hinrichsen 1987:59); 26% of these forests were in North America. Because of the growing worldwide demand for wood products, increasing pressure is being placed on older growth forests. In many parts of North America, timber harvest levels approach or have exceeded sustainable levels. Postel and Heise (1988) reported that between 1963 and 1982, forest cover in the contiguous United States dropped 10%, to 233 million ha. The United States and Canada accounted for 35% (590 million m³) of the worldwide production of coniferous tree species in 1988, and demand levels are projected to increase 18–53% by 2030 (Postel and Ryan 1991). Marten are habitat specialists (Bissonette et al. 1989, Brainerd 1989), occurring primarily in mature coniferous habitat (Soutiere 1979, Steventon and Major 1982, Raine 1983, Bateman 1986), and their population status and health are linked closely to forest trends. As mature coniferous forest is cut and replaced by early seral stages, marten habitat is lost. The impacts are most severe in winter because marten require subnivean access to their prey. Only older growth forests with accumulated CWD provide the forest floor structure necessary to enable marten to forage effectively during winter. Managers need to be cognizant of the large-scale cumulative effects of habitat alteration to avoid long-term population declines in core sensitive species (Bissonette et al. 1989) such as marten.

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SEXUAL SEGREGATION AND FEMALE GRIZZLY BEAR AVOIDANCE OF MALES

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Abstract: We examined seasonal use of habitat for 14 male and 5 female grizzly bears (*Ursus arctos*) in southwestern Alberta, 1981–84, to test 2 competing hypotheses regarding segregation of the sexes. The male avoidance hypothesis predicts increasing differences in use of habitat with increasing male use of female-occupied areas because of female avoidance of males. The no avoidance hypothesis predicts decreasing differences in use of habitat with increasing male use of female-occupied areas because of increasing similarity of available habitat. Differences in use of habitat were greatest during late summer, when many males concentrated in the female-occupied area, and they were less during other seasons when few males were in the female-occupied area. Three of 4 habitat variables differed ($P \leq 0.10$) between the sexes during late summer, whereas 2, 1, and 2 variables differed during spring, early summer, and autumn, respectively. Grizzly bear females segregated from males and data support the hypothesis that females avoid males. If females avoid males and male-occupied habitats, reproduction could decline because of nutritional deprivation and survival could decline because of their increased use of human-occupied areas.

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Grizzly bears have disappeared from most of their historic range, largely by incremental population and habitat losses at the contracting edges of the species' range (Servheen 1990). In Alberta, there were an estimated 780 grizzly bears in 1990, and numbers were declining (Servheen 1990). Nagy and Gunson (1990) estimated 62 grizzly bears in southwestern Alberta, the edge of the species' range. In this study, we radio-monitored 19 of 38 bears in a declining population of Kananaskis Park and Bow Crow Forest, southwestern Alberta (Wielgus and Bunnell 1994). We must understand use of habitat and

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