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Source: *The Journal of Wildlife Management*, Jan., 1989, Vol. 53, No. 1 (Jan., 1989), pp. 191-196

Published by: Wiley on behalf of the Wildlife Society

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WINTER RESTING SITE ECOLOGY OF MARTEN IN THE CENTRAL ROCKY MOUNTAINS

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Abstract: We investigated the resting site ecology of American marten (*Martes americana*) in the central Rocky Mountains during 2 winters, 1985–86 and 1986–87. We found 8 marten used 57 resting sites on 141 occasions. Marten rested primarily in subnivean sites associated with coarse woody debris, including logs and stumps. Use of spruce (*Picea* spp.)–fir (*Abies lasiocarpa*) stands by adults was greater than expected and use of lodgepole pine (*Pinus contorta*) stands was less than expected on the basis of spatial availability. Juveniles used stand types in proportion to spatial availability. Fidelity to individual resting sites and to subnivean sites associated with coarse woody debris was highest among adults. Type of resting site used depended on air temperature at the time of resting; above-snow sites were used during the warmest weather, and subnivean sites associated with coarse woody debris were used during the coldest weather. Marten rested for longer periods where coarse woody debris formed all or part of the resting site than they did at other sites. Log densities were higher and mean log diameters greater in spruce–fir stands than in lodgepole pine stands. Resting sites associated with coarse woody debris occurred primarily in spruce–fir stands, whereas other resting sites occurred in other stand types. Resting sites were closer to streams and lakes than expected. The importance of resting where coarse woody debris is available to provide thermal cover may explain the apparent dependence of marten on old-growth forest in the central Rocky Mountains in winter.

J. WILDL. MANAGE. 53(1):191–196

Resting sites used by American marten have been described for a wide range of geographic locations and include a variety of natural and man-made microhabitats (Campbell 1979, Steventon and Major 1982, Martin and Barrett 1983, Buskirk 1984). Locations of resting sites range from the forest canopy to beneath the soil surface. Winter resting sites are often associated with coarse woody debris (CWD), including logs, stumps, and snags (Steventon and Major 1982, Martin and Barrett 1983, Spencer 1987). In summer, marten generally rest in sites above the ground, often in the canopy layer (Masters 1980, Burnett 1981, Martin and Barrett 1983).

Temporal differences in resting site preferences could be explained by thermoregulatory needs of marten, or by other factors such as vulnerability to predation. Marten live where above-snow air temperatures (T_a) in winter are lower than their lower critical temperature (T_{lc} = the temp at which an animal must increase its metabolic rate above resting levels to offset thermal losses [16 C]) (Buskirk et al. 1988) by ≤50 C. Thus they would appear to pay high energetic costs to rest at or near T_a in winter.

Marten are associated with late successional stands of conifer-dominated forest over a wide geographic area (Francis and Stephenson 1972, Koehler and Hornocker 1977, Simon 1980, Bateman 1986) and have a close and seemingly obligatory association with old-growth stands in the Rocky Mountains in winter (Campbell 1979). However, a clear understanding of why marten are associated with old-growth is lacking. Patterns of use of resting sites may provide a better understanding of the apparently obligatory nature of this association. We report on characteristics of resting sites used by marten in the Medicine Bow Mountains, Wyoming during 2 winter field seasons. We identify environmental and behavioral correlates of resting site use and draw inferences about the importance of resting site types for thermoregulation. We also discuss the importance of CWD as a resting site component in understanding the old-growth dependency of marten during winter.

L. R. Forrest provided invaluable assistance during the winter field studies. We appreciate the cooperation of R. H. Abell, for allowing use of a portion of his trapline for field work. This research was supported by the Committee for Research and Exploration, National Geographic Society, the U.S. Forest Service (USFS), Rocky Mountain Forest and Range Experiment Station, and the Office of Research, University of Wyoming. We thank the Wyoming Game and

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Fish Department for technical support, and the University of the Wilderness, Evergreen, Colorado for use of the Snowy Range Laboratory.

STUDY AREA

We conducted field work in the Medicine Bow Mountains of southeastern Wyoming from November 1985 to February 1986 and from November 1986 to February 1987. The study area was located on the eastern slope of the Snowy Range (41°18'N, 106°15'W) and extended from 2,550 to 3,300 m in elevation. Two principal forest types were dominated by lodgepole pine, and the other by Engelmann spruce (*Picea engelmannii*) and subalpine fir. The 2 zones were separated elevationally, with spruce–fir dominant >2,800 m, but generally restricted to riparian habitats <2,800 m (Moir 1969, Fahey 1983). Lodgepole pine is a seral precursor to spruce–fir on mesic sites, but represents the climax form on many xeric and south-facing sites. Spruce–fir stands contained many trees >1 m diameter at breast height (dbh) and >400 years old (Oosting and Reed 1952). These stands were uneven aged, held large volumes of CWD in the form of snags, stumps and downed logs, and met the criteria proposed by Franklin et al. (1981) for old-growth forest. Lodgepole-dominated stands, in contrast, had been harvested intensively during the late nineteenth century and had been burned intermittently (Billings 1969), resulting in a mosaic of stand ages and characteristics. Lodgepole stands were generally more even aged and had fewer large trees than spruce–fir stands.

The vertebrate fauna of the area was typical of the Canadian life zone of the central Rocky Mountains (Long 1965, Raphael 1987). Red squirrels (*Tamiasciurus hudsonicus*) were common throughout mid-aged and older conifer-dominated stands and constructed elaborate underground nests within piles of conifer cone bracts (middens). Long-term data provided by 4 weather stations maintained within the study area by the Wyoming Water Research Center indicated a mean annual precipitation of about 600 mm, 66% of which falls as snow. Mean midwinter snow depths (at 3,000 m) averaged 1.92 m in 1985–86, and 0.95 m in 1986–87. Long-term mean monthly T_a at 2,460 m for December, January, and February was −4.4, −5.6, and −5.0 C, respectively (Becker and Alyea 1964).

METHODS

We captured animals in baited live traps (Models 105 and 106, Tomahawk Live Trap Co., Tomahawk, Wis.) from late November to early January of each year. Each marten was anesthetized, equipped with a radio collar (BT type, AVM Instrument Co., Livermore, Calif.) weighing approximately 29 g, and surgically implanted with a 16-g temperature-sensitive transmitter (Model L, Mini-mitter Co., Sunriver, Oreg.) for concurrent studies of body temperature dynamics (Buskirk et al. 1988). The animals were released at capture sites after recovering fully from the anesthesia, 3–16 hours after surgery. All marten were recaptured, collars removed, and an upper premolar extracted for aging by staining and counting cementum annuli (Grue and Jensen 1979) at the completion of the study. No animals studied the first winter were captured the second year. We classified animals <1 and >1 year old as juveniles and adults, respectively. Radiotracking of animals with directional antennas was conducted during daylight hours. We marked locations of resting sites and made habitat measurements on return visits to each site. We placed automated telemetry receivers near resting sites to record movement to and from the sites and determine times of onset and termination of individual resting episodes. Each automated unit consisted of a receiver (Mini-mitter Co., Sunriver, Oreg.), a timing device that permitted us to set duration and interval between sampling periods, and a cassette recorder. We sampled transmitter signals for 1 minute every 15 or 30 minutes. Weather variables were recorded at automated climate stations maintained by the Wyoming Water Research Center. Temperatures of forest microenvironments were recorded by means of thermocouples placed before the first snowfall, and a Campbell 21X data logger (Campbell Scientific, Logan, Ut.). We monitored temperatures at 15-minute intervals at 3 subnivean cavities covered by CWD, 2 cavities in snags above the snow surface, and at 2 sites in the canopy layer. At the completion of each field season, most resting sites, excluding those in rock fields, were excavated to determine where marten had rested in relation to subnivean structures. We used single-factor analysis of variance (ANOVA) to test for differences in T_a when animals rested in different site types. To determine use and availability of habitat types for resting we es-

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Table 1. Numbers of resting sites and resting episodes by marten in the Medicine Bow Mountains, Wyoming, winters 1985–86 and 1986–87. Mean above-snow air temperatures (T_a) (C) for complete resting episodes (n = 72) involving each type of site are presented.

		Rock field below snow surface			Coarse woody debris below snow surface			Above snow surface		
Age	n	No. resting sites	No. resting episodes	T_a	No. resting sites	No. resting episodes	T_a	No. resting sites	No. resting episodes	T_a
Juv	5	9	21		17	38		10	11	
Ad	3	2	3		11	51		1	1	
Total	8	11	24	−2.2	28	89	−5.5	11	12	−0.9

tablished a rectangular study area of 69.2 km^2 around the outermost resting sites, and sampled 150 points selected by random grid coordinates. Boundaries and classifications of mapped stands are those of the USFS Resource Inventory System data base, Medicine Bow National Forest. We compared the use of stand types with availability by Chi-square goodness-of-fit tests followed, in case of significance ($P \leq 0.05$), by observed and expected comparisons of individual cell values using the Bonferroni Z-statistic (Neu et al. 1974). We estimated spatial density of CWD on the forest floor from subscores of old-growth score cards completed as part of USFS stand inventories. Subscores represented ocular estimates of mean diameter of downed logs on a 0–5 scale and density of logs >0.18 m in diameter on a 0–4 scale. Midpoints of log-diameter categories were 76, 203, 279, 356, and 483 mm. Midpoints of log-density categories were 1.2, 8.4, 20.4, and 30.0 logs/ha. Ranks of log density and log diameter were compared for 100 randomly selected stands classified as lodgepole and 100 as spruce–fir.

RESULTS

We found 8 marten (3 ad M, 3 juv M, and 2 juv F) in 57 resting sites on 141 occasions over 2 winter field seasons (Table 1). Study animals were not found on a mean of 31.8% of the days on which we searched for them; resting sites reported herein were a subset of those used. Forty-nine percent of resting sites and 63.1% of resting episodes were in subnivean sites associated with CWD. These sites were more often adjacent to than inside logs or stumps (Fig. 1). Nineteen and 17% of all resting sites and resting episodes, respectively, were in rock fields. Of all resting sites found, 42% were in stands classified as lodgepole pine, 42% in spruce–fir, and 16% in other stand types (Table 2). This compared with spatial availabilities of 48% for lodgepole pine, 23% for spruce–fir, and 29% for other stand types. Adult resting episodes and resting episodes for juveniles and adults occurred more often than expected in spruce–fir and less often than expected in lodgepole stands (Table 2). Stand preferences as indicated by resting episodes depended on age; adult marten selected for spruce–fir stands more strongly than did juveniles ($\chi^2 = 30.3$, 2 df, $P < 0.001$). Juvenile resting episodes occurred in stands in proportion to spatial availability.

Up to 14 resting sites were found/marten. Fidelity to resting sites was greater for adults than for juveniles. Seventy-one percent of adult resting episodes involved reuse of sites, whereas 54% of juvenile resting episodes were in sites not observed to be used before ($\chi^2 = 8.7$, 1 df, $P = 0.003$). The longest consecutive use of a resting site by a marten was 8 days. Five resting sites were intermittently reused throughout the period over which they were monitored (approx 53 days), whereas 34 resting sites were used only once. Despite use of some areas by >1 marten, use of a resting site by >1 marten, was not observed.

Marten used resting sites associated with CWD a mean of 2.9 times over the study period, compared with 1.6 times for other types of sites ($U = 492$, $P = 0.14$). The type of resting site used was related to T_a at the time of the resting episode. Mean T_a when marten rested above the snow was −0.9 C versus −2.2 C when they rested in rock field sites, and −5.5 C when they rested in other subnivean site types (mostly associated with CWD; ANOVA, $F = 5.3$, 71 df, $P = 0.007$). Microenvironmental temperature (T_{me}) for subnivean sites showed small variations within the range −0.5–−2.5 C over the study period and were similar for both years, while above-snow T_a (including cavities in snags)

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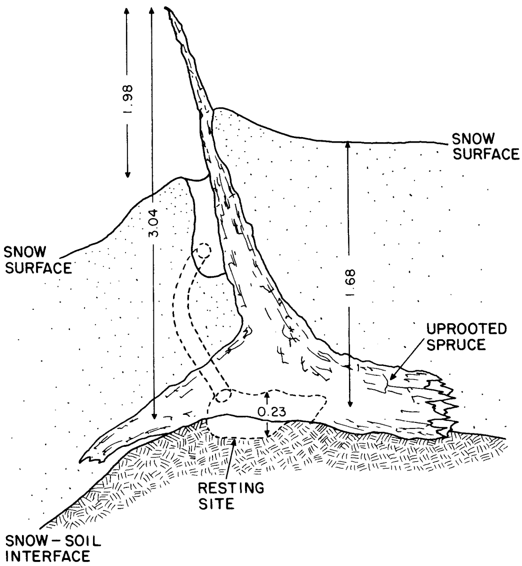

Fig. 1. Side view of resting site used by marten during winter 1985–86 (excavated 31 Jan 1986) in relation to uprooted spruce and snow layer. Partially decomposed wood formed the roof of the resting chamber. Dimensions are in meters.

ranged from −28 to 9 C. Further, the stand type in which marten rested was related to the minimum above-snow T_a on the day when the stand was used for resting. The mean minimum T_a on days when marten rested in stands classified as lodgepole was −8.7 C, in spruce–fir stands −11.3 C, and in other stand types −11.6 C (F = 3.1, 140 df, P = 0.05). A significant relationship existed between resting site type and stand type. Seventy-five percent of resting sites associated with CWD were located in spruce–fir stands, whereas 67% of resting sites not associated with CWD were in nonspruce–fir stands (χ^2 = 9.6, 1 df, P = 0.002). Spruce–fir stands had larger-diameter logs on the forest floor ($\bar{x}$ = 0.27 m) than did lodgepole stands ($\bar{x}$ = 0.19 m) (U = 2,754, P < 0.001) and spruce–fir stands had higher densities of logs >0.18 m in diameter ($\bar{x}$ = 13.2/ha) than did lodgepole stands ($\bar{x}$ = 6.2/ha) (U = 3,868, P = 0.003). Resting episodes were longer in subnivean sites associated with CWD ($\bar{x}$ = 10.4 hr) than in rock fields ($\bar{x}$ = 4.5 hr) or in above snow sites ($\bar{x}$ = 3.6 hr) (F = 3.2, 71 df, P = 0.05).

The distribution of resting sites was characterized by proximity to surface water. Resting sites were significantly closer to streams or lakes ($\bar{x}$ = 173 m) than expected from the distances ($\bar{x}$ = 262 m) between streams and lakes and 150 randomly chosen points within the study area (F = 7.44, 206 df, P = 0.007).

DISCUSSION AND MANAGEMENT IMPLICATIONS

Patterns of use and reuse of resting sites by marten in the patchy habitat in our study area provide evidence that marten discriminated in their use of resting sites, and that suitable resting sites were not omnipresent in marten home ranges. The importance of thermal cover to marten, particularly during severe winter weather, has been described by Buskirk et al. (1988). We found, as did Spencer (1987), that the most important winter resting sites were in subnivean locations partially or entirely surrounded by CWD. We believe the use of subnivean sites is attributable to the warm (relative to T_a) subnivean environment. Resting in subnivean sites and in spruce–fir stands was most common during periods of the coldest weather, when marten rested for longer periods than they did during warm weather (Buskirk et al. 1988). All of the winter resting sites that we found would have provided protection against likely predators (e.g., coyote [*Canis latrans*] and great horned owl [*Bubo virginianus*]). Our data demonstrated use of sites that provided the highest T_{me} during the coldest weather and we conclude that marten used sites primarily on the basis of

Table 2. Numbers of resting sites and numbers of resting episodes by marten and spatial availability (%) of principal stand types in the Medicine Bow Mountains, Wyoming, winter 1985–86 and 1986–87.

	Lodgepole	Spruce–fir	Other[a]	χ^2	P
Resting sites	24	24 +[b]	9	69.3	<0.001
Resting episodes (juv)	33	16	16	0.7	>0.50
Resting episodes (ad)	14 −	54 +	8	101.0	<0.001
Resting episodes (total)	47 −	70 +	24	58.5	<0.001
Spatial availability	48.0	22.7	29.3		

[a] Other stand types included rangelands and unclassified stands.
[b] Use was compared with availability using Chi-square analysis. If use was different from availability (P < 0.05) the use of individual stands was evaluated with the Bonferroni Z-statistic. Symbols indicate use greater (+) or less (−) than expected.

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the thermal properties of those sites. Juvenile marten in this study were likely to rest above the snow surface on warm days, when $T_a > T_{me}$ of subnivean sites. Marten tended to rest in subnivean sites when T_a was colder than T_{me} of subnivean sites. Thus, marten appeared to minimize their rates of energy loss by alternating between resting site types in response to T_a to minimize body temperature–T_{me} gradients. Because marten possess limited energy reserves in winter (Buskirk and Harlow 1989) and are not morphologically adapted to minimize heat loss (Buskirk et al. 1988), alternating between resting site types would appear to be highly adaptive. Pulliainen (1981) noted the tendency of pine marten (*Martes martes*) in Fennoscandia to make greater use of subnivean resting sites in colder, more northern areas than they did farther south.

We postulate that use of subnivean sites associated with CWD during the lowest T_a is due to the ability of these sites to trap small air spaces and to the low thermal conductivity of partially decomposed CWD relative to soil and rock. In no instance did we find marten resting in subnivean pockets completely surrounded by snow; Spencer (1981) and Pulliainen (1981) made similar reports. Snow has a very low thermal conductivity (Pruitt 1978), but has a major shortcoming as a structural part of resting sites; its melting point is lower than the T_{lc} of winter-acclimated marten. Thus, if marten were to rest in pockets surrounded by snow, we predict that heat lost from the body surface would not be able to warm the pocket to thermoneutrality, but would result in melting of snow and wetting of the fur. We predict that CWD in intermediate stages of decomposition has important thermal properties that cause marten to prefer it as a structural component of resting sites. Specifically, we predict that low thermal conductivity of partially decomposed CWD makes it possible for marten to warm resting sites by the loss of body heat, and that this warming of resting sites facilitates resting metabolic rates within a thermoneutral environment.

Stand preferences for resting by adult marten appear to be due to the greater availability of subnivean CWD in spruce–fir than in other stand types. The reason for the proximitiy of resting sites to streams and lakes is less clear. Stand types preferred by marten for resting may be favored by the physiography of small drainages, or by historical cutting practices that resulted in the preservation of spruce–fir stands near streams. In addition, aggregates of CWD are commonly found in steep-sloped, upper level riparian areas through the natural downhill movement of windthrow and earthflow (Harmon et al. 1986). Higher relative volumes of CWD in these settings may provide a greater number of potential resting sites. Also, prey availability is likely higher in riparian settings than elsewhere, either because prey densities are higher (Tevis 1956, Ream and Gruell 1979), or because structural features, including CWD, render subnivean prey more accessible to marten. Energetic benefits would appear to accrue to marten from resting near foraging areas, especially during periods of severe cold. Other studies have found marten attracted to riparian habitats (Simon 1980, Spencer et al. 1983, Hargis and McCullough 1984).

Adult marten rested more often in spruce–fir than in other stand types and showed high fidelity to individual sites. However, juveniles rested mostly in lodgepole stands and showed less fidelity to individual resting sites. Two factors may account for these observed age differences in stand preferences and resting site fidelity. Adults may exclude juveniles from preferred resting areas so that juveniles are limited to lodgepole stands with little CWD. Alternatively, juveniles may lack experience in selecting the best resting sites or in recognizing the habitats in which desirable sites occur, necessitating attempts to find better sites. We predict that the pattern of resting site use exhibited by juveniles on our study area caused them to incur higher energetic costs than adults during resting.

Patterns of resting site use by marten demonstrate the importance of CWD as a habitat component in winter. Position in relation to the snow surface is an important criterion in resting site selection, and CWD appears to be an important structural part of resting sites, especially in cold weather. Woody debris is a defining feature of old-growth forest (Franklin et al. 1981). Therefore, the resting site requirements of marten illustrate thermoregulatory adaptations and help to explain the reported association of this forest carnivore with old-growth forest during the cold season.

Our findings suggest the importance of managing for CWD in forest communities where maintenance of winter resting habitat for marten is an objective. Spruce–fir stands were important resting habitat for marten because of

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the availability of CWD. Thus, the retention of spruce–fir stands and the dispersion of those stands in relation to foraging areas in the central Rocky Mountains may have important implications for marten populations. Because of its role in forming winter resting sites, the size, shape, and physical properties of CWD, and its position in relation to the snow surface, are important habitat features for marten and should be considered when managing for them.

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Received 10 February 1988.
Accepted 27 July 1988.

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