

WINTER HABITAT SELECTION BY AMERICAN MARTEN (Martes americana)

IN NEWFOUNDLAND: WHY OLD GROWTH?

by

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Abstract

Although the American marten (Martes americana) generally is recognized as an obligate late-seral species, the factors dictating this close association are poorly understood. A population of martens in Newfoundland were studied for 2 years using snow tracking. As expected, use of habitat types was not proportional to availability ($P < 0.001$). Defoliated and late-seral conifer stands were used more than expected, while all other types indicated expected or less than expected use. Habitat selection by martens was detectable at spatial scales greater than 80 m ($P < 0.001$).

Newfoundland martens were radio-collared and monitored for diel activity during the winters of 1990 and 1991. A regression of the percent active fixes on temperature had a negative slope ($b = -4.45$, $P = 0.084$, $n = 12$), indicating that martens did not minimize their exposure to low temperatures. A log-linear model suggested that the presence or absence of light was the only factor associated with marten activity patterns ($P < 0.001$).

Martens in Western Newfoundland and a population in Yellowstone National Park were tested for their response to predation risk using bait stations based in various habitat types. Visitation rates of martens at bait-boxes were not significantly different between study sites ($P = 0.190$). However, martens visitation by habitat was different ($P = 0.001$). I detected no difference in the use of bait-boxes by martens in old growth and defoliated habitats, suggesting that foliar cover may not have a strong influence on the risk of predation for martens during winter. However, martens used bait-boxes in old growth to

a greater extent than those in open habitats ($P < 0.001$), suggesting that they perceived stem structure as decreasing predation risk.

In captive experiments conducted during the summer of 1993, martens selected areas with both overhead cover and woody stem structure ($P = 0.012$). I detected no difference between the use of areas with only overhead cover and those having only stem structure ($P = 0.671$). However, martens decreased foraging activity in response to a predatory cue, ($P = 0.004$). The inability of martens to use food resources in areas lacking cover during the summer suggests a perception of increased threat associated with these areas.

(100 pages)

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May you live in a world where wilderness is not a luxury and education is as treasured as any possession. I will try and provide support for your dreams and a shoulder for your sorrow. Remember that life is precious and your joy passing through it will be based on whom you share it with.

Gary S. Drew

FOREWORD

This dissertation is presented in 5 chapters. Chapter I is a comprehensive introduction and chapter V a comprehensive conclusion both of which were formatted in the style of the *Journal of Wildlife Management*. My research was organized into the 3 middle chapters (II-IV), each dealing with some aspect of this question. These chapters have been formatted in the style of the *Journal of Wildlife Management* (chapter II), the *Canadian Field-Naturalist* (chapter III), and *Animal Behavior* (chapter IV). Literature citations, tables, and figures are organized within individual chapters.

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CHAPTER I

INTRODUCTION

The reduction in old growth forest throughout the world has led to increased research and debate concerning old growth communities (Harris 1984). In addition to the absolute reduction of old growth habitat, obligate old growth species are confronted with the added effects of fragmentation of remaining habitat (Harris 1984, Wilcox 1980). As a result, these species are highly susceptible to decreases in genetic diversity and local extirpation or extinction. These problems are especially acute for carnivores, such as American marten (Martes americana), that occur in relatively low densities. The loss of mature and older coniferous forests characterized by overhead cover has been cited as one of the major factors responsible for the reduction in numbers of martens in much of North America (Davis 1983, Thompson 1991). Historical harvest data show synchronous declines in martens with the loss of first-growth forest in North America (Novak et al. 1987).

Numerous studies have shown a pattern of close association between martens and coniferous forests containing large trees and abundant coarse woody debris (CWD) (Koehler and Hornocker 1977, Mech and Rodgers 1977, Cambell 1979, Soutiere 1979, Steventon and Major 1982, Spencer et al. 1983, Zielinski et al. 1983, Bateman 1986, Snyder and Bissonette 1987). However, recent work in Maine indicates that although martens are associated with later seral stage coniferous forest at the landscape scale, their smaller scale selection is broader than originally thought (D. Harrison, pers. commun.). Recognition of the relationship between martens and their preferred habitats has led to the use of martens as an indicator species for mature boreal forest by the U.S. Forest Service. Although martens

are habitat specialists, the factors limiting martens to coniferous forests have not been tested quantitatively.

Marten habitat association has been attributed to: (1) the abundance of prey in old growth habits (Koehler and Hornocker 1977), (2) abundant access to subnivean resources during the winter (Raine 1982, Steventon and Major 1982, Hargis and McCullough 1984, Bissonette et al. 1988, Buskirk et al. 1989, Sherburne and Bissonette 1994), and (3) decreased predation risk while in late-seral forest (Pulliainen 1981, Thompson 1991).

The evidence for martens selecting coniferous forest habitats because of higher prey abundances is ambivalent. While many of the species common in the diets of martens are found in forested habitats, others including the meadow vole (*Microtus pensylvanicus*), lagomorphs, and various berries typically reach higher densities in more open habitats. If martens were selecting areas based on prey availability alone, I would expect the habitat use of martens to change during population lows of their most common prey. For example, meadow vole populations on Newfoundland crashed in the summer of 1987 (Bissonette et al. 1988, Tucker 1988). However, martens still made only limited use of the abundant raspberry fruits available in clear-cuts (Bissonette et al. 1988) and their movements indicated avoidance of newly cut areas (Fredrickson 1990). While forage resources are undoubtedly important in the habitat use of martens, this appears to offer only a partial explanation for the habitat selection of martens.

The use of subnivean access points by martens is well documented (Buskirk et al. 1989, Corn and Raphael 1992, Sherburne and Bissonette 1993). Coniferous forests typically possess a variety of structural components, including moderate to high canopy closure, large

stems, and abundant coarse woody debris (CWD), that interact with snowfall to provide numerous access points. A long thin body, minimal body fat reserves, and short pelage allow martens to make use of breaks in the snow layer to access subnivean resources (Brown and Lasiewski 1972, Buskirk 1984, Buskirk et al. 1989). However, snow tracking data have shown that martens use only a small subset of the available access points (Sherburne 1992, Sherburne and Bissonette 1993, Thompson and Colgan 1994). Snow tracking also has revealed that martens often circumvent even very small tree-gaps in late-seral forest (G. Drew and J. Bissonette, Utah State Univ., unpubl. data). Availability of subnivean access certainly is not lacking in older forests (Sherburne 1994) and plays a role in the habitat selection of martens during winter, however avoidance of treeless gaps in the forest begs another explanation. If access to resources was the only selection pressure on martens, I would expect the affinity of martens for coniferous forests to be primarily a winter phenomenon. This is certainly not the case.

Although previous researchers have noted that martens may be sensitive to predation risk (Hargis and McCullough 1984, Thompson 1991), these hypotheses have yet to be tested. While martens must balance requirements for foraging and thermal homeostasis with risk of predation, the asymmetric costs of predation would strongly bias a long-lived species, such as American marten, toward overestimation of predation risk (Bouskila and Blumstein 1992).

Characteristic American marten habitat, i.e., coniferous forests, provide 2 conspicuous physical components that could serve as security from predation, (1) foliar cover, i.e., leaves, and (2) stem structure, i.e., live stems, snags, and CWD. The Habitat Suitability

Index model (HSI) developed by the U.S. Fish and Wildlife Service employs measures of overhead cover and coarse woody debris to grade habitat quality (Allen 1984). However, since foliar cover and stem structure may be associated, their independent influence on the habitat use of martens is poorly understood. The relatively dense canopies of late-seral stands may provide martens with required cover from avian predators (Pulliainen 1981, Hargis and McCullough 1984). This could be especially important during the winter months when their dark brown winter pelage contrasts with snow cover (Pulliainen 1981). There is limited evidence of avian predation on American martens. However, attacks on martens in Newfoundland by hawk owl (Surnia ulula) (Bissonette et al. 1988) and in California by prairie falcon (Falco mexicanus) (Murie 1961) have been recorded. Predation by raptors also has been documented for M. martes in Finland (Pulliainen 1981). Stem structure has been linked to escape cover. Pulliainen (1981) observed that late-seral trees also provided pine martens with escape cover from red fox. The characteristic practice of climbing trees to escape terrestrial predators could also explain early anecdotal accounts of martens as primarily arboreal. This view was generally accepted until the 1950s when researchers looked closely at the movements of martens and found them to be almost exclusively terrestrial (Hawley and Newby 1957).

Newfoundland pine martens (M. a. atrata) were once found in most forested areas of the island (Bergerud 1969, Snyder, unpubl. data), but by 1934 they were sufficiently rare to require a closing of the trapping season (J. E. Snyder, Nfld. Wildl. Div. unpubl. data). Even with this protection, martens appear to have been extirpated from eastern Newfoundland by 1969 (Bergerud 1969). In 1973, a Pine Marten Study Area (PMSA) was created by the

Newfoundland and Labrador Wildlife Division as a refuge, where all trapping and snaring was prohibited to protect the last known population of martens on the island. Although the marten population within the PMSA has remained relatively stable, estimated at approximately 150 resident adults, martens have not been able to disperse and colonize surrounding areas (Bissonette et al. 1988). In response to their steady decline in numbers and distribution, martens in Newfoundland were listed as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in April of 1986.

No detailed study of American marten survival in the wild exists, but previous studies in the PMSA found predation resulted in at least 3 mortalities of martens (Bissonette et al. 1988). A red fox appeared to have partially consumed 1 marten. The other 2 mortalities could not be attributed definitively to any species, though 1 was being fed on by a raven (Corvus corax). In Yellowstone National Park, Sherburne (pers. commun.) documented 2 martens killed in traps by coyotes (Canus latrans). Given the cryptic nature and wide dispersal patterns of martens, it is not surprising that reports of predation are rare.

The goals of this study were first, to describe the activity and habitat use patterns of Newfoundland martens and test them for adherence to the predictions of the 3 hypotheses explaining the obligate use of late-seral habitats. Secondly, to investigate the relative risk associated with various combinations of foliar cover and stem structure in late-seral forest. Combinations of field observations, field experiments, and captive experiments were used to investigate how the habitat selection criteria of martens were influenced by predation risk in Newfoundland, Yellowstone National Park, and Utah.

LITERATURE CITED

- Allen, A. W. 1984. Habitat suitability index models: marten. U.S. Fish and Wildl. Serv. FWS/OBS-82/10.11. Washington D.C. Revised. 13 pp.
- Bateman, M. C. 1986. Winter habitat use, habits and homerange size of the marten, Martes americana, in western Newfoundland. Can. Field-Nat. 100:58-62.
- Bergerud, A. T. 1969. The status of pine marten in Newfoundland. Can. Field-Nat. 83:128-131.
- Bissonette J. A., R. J. Fredrickson, and B. J. Tucker. 1988. The effects of forest harvesting on marten and small mammals in western Newfoundland. Newfoundland and Labrador Wildl. Div., and Corner Brook Pulp & Paper Co., Ltd. Utah Cooperative Fish and Wildl. Res. Unit, Utah State Univ., Logan, UT. 109 pp.
- Bouskila, A., and D. T. Blumstein. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. Am. Nat. 139:161-176.
- Brown, J. H., and R. C. Lasiewski. 1972. Metabolism of weasels: the cost of being long and thin. Ecology 53: 939-943.
- Buskirk S. W. 1984. Seasonal use of resting sites by marten in south-central Alaska. J. Wildl. Manage. 48:950-953.

- _____, S. C. Forrest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting ecology of marten in the central Rocky Mountains. *J. Wildl. Manage.* 53:191-196.
- Cambell, T. M. 1979. Short-term effects of timber harvests on pine marten ecology. M.S. Thesis, Colorado State Univ., Ft. Collins. 71 pp.
- Corn, J. G., and M. G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. *J. Wildl. Manage.* 56:442-448.
- Davis, M. H. 1983. Post-release movements of introduced marten. *J. Wildl. Manage.* 43:850-860.
- Fredrickson, R. J. 1990. The effects of disease, prey fluctuation, and clear-cutting on American marten in Newfoundland, Canada. M.S. Thesis, Utah State Univ., Logan. 64pp.
- Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. *J. Wildl. Manage.* 48:140-146.
- Harris, L. D. 1984. The fragmented forest: island biogeography and the preservation of biotic diversity. Univ. Chicago Press. 211 pp.
- Hawley, V. D., and F. E. Newby. 1957. Marten homeranges and population fluctuations. *J. Mammal.* 38:174-184.

- Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *J. Wildl. Manage.* 41:500-505.
- Mech, L. D., and L. L. Rodgers. 1977. Status, distribution and movements of martens in northeastern Minnesota. USDA For. Serv. Res. Paper NC-143, North Cent. For. Exp. Sta., St. Paul, Minn. 7 pp.
- Murie, A. 1961. Some food habits of the marten. *J. Mammal.* 42: 516-521.
- Novak, M., J. A. Baker, M. E. Obbard, B. Malloch. 1987. *Furbearer Harvests in North America: 1600-1984.* Ontario Trappers Assoc., North Bay, Ontario. 270 pp.
- Pulliainen, E. 1981. Winter habitat selection, home range, and movements of the pine marten, Martes martes in a Finnish Lapland forest. Pages 1068-1087 in J. A. Chapman and D. Pursley, eds. *Proc. Worldwide Furbearer Conf.*, Frostburg MD. Johns Hopkins Press, Baltimore, MD.
- Raine, R. M. 1982. Ranges of juvenile fisher, Martes pennanti, and marten, Martes americana, in southeastern Manitoba. *Can. Field-Nat.* 96:431-438.
- Sherburne, S. S. 1992. Marten use of subnivean access points in Yellowstone National Park, Wyoming. M.S. Thesis, Utah State University, Logan. 37pp.
- _____, and J. A. Bissonette. 1993. Squirrel middens influence marten (Martes americana) use of subnivean access points. *Am Mid. Nat.* 129:204-207.

_____, and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. *J. Wildl. Manage.* 58:400-405.

Snyder, J. E., and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. *Can. J. Zool.* 65:169-174.

Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. *J. Wildl. Manage.* 43:850-860.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. *J. Wildl. Manage.* 47:1181-1186.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. *J. Wildl. Manage.* 46:175-182.

Thompson, I. D. 1991. Could marten become the spotted owl of eastern Canada? *Forest. Chron.* 67:136-140.

_____, and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. *J. Wildl. Manage.* 58:280-288.

Tucker, B. J. 1988. The effects of forest harvesting on small mammals in western Newfoundland and its significance to marten. M.S. Thesis. Utah State Univ., Logan. 49pp.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95-117 in M. E. Soule and B. A. Wilcox, eds., Conservation biology, an evolutionary-ecological perspective. Sinauer Associates, Inc., Sunderland, Mass.

Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. *J. Mammal.* 64:387-396.

CHAPTER II

WINTER HABITAT SELECTION BY AMERICAN MARTEN IN NEWFOUNDLAND: MULTIPLE-SCALE ANALYSIS¹

Abstract: Scale dependency in winter habitat use by American martens (Martes americana) in Newfoundland, Canada was studied during the winters of 1990 and 1991. Martens were snow tracked (35.5-km) and 193 global positioning system locations collected. Integration of highly accurate snow tracking data with satellite imagery enabled the development of a spatially explicit method for examining the scale at which selection was detectable. Landscape-scale habitat use was not in proportion to habitat availability in the study area based on a null model simulation ($P < 0.004$). Mature and defoliated conifer stands were used more than expected. Habitat composition differed between marten trails and habitats at distances greater than 80 m from used habitats ($P < 0.001$). Analysis of buffers around randomly distributed transects suggested the probability of this result by chance was $P = 0.024$. Although analyses of habitat selection at both the landscape and trail buffer scales detected selection of mature and defoliated stands by martens, the magnitudes of selection varied considerably. In particular, landscape-scale measurements underestimated the avoidance of broad-leaf- dominated habitats.

¹Coauthored by Gary S. Drew and John A. Bissonette

The chosen habitat of any species is a collection of environmental features that provide adequate resources for its continued survival. However, the scale at which habitat use is examined can influence results and interpretations (Johnson 1980, Harrison et al. In Press). American martens (Martes americana) generally are associated with late-seral conifer and mixed conifer-hardwood forests (Koehler and Hornocker 1977, Mech and Rodgers 1977, Cambell 1979, Soutiere 1979, Steventon and Major 1982, Spencer et al. 1983, Bateman 1986, Snyder and Bissonette 1987). However, our understanding of how martens use habitats has been based primarily on (1) telemetry studies that reflect a wider home-range scale and (2) snow tracking of martens that, by itself, cannot provide a context or scale within which movement decisions are made. Although snow tracking can provide precise locational data, without knowledge of the availability of surrounding habitats, identification of habitat selection is difficult. The incorporation of a context-sensitive measurement of habitat selection, i.e., one that takes surrounding habitats into account, is needed. As an added benefit, this approach may be used to assess the scale at which habitat decisions are made.

This study was initiated in response to a steady decline of American martens (M. a. atrata) on the island of Newfoundland. In April 1986, Newfoundland martens were listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (J. E. Snyder, Nfld. Wildl. Div. unpubl. data). My objectives were to (1) determine the scale of habitat selection exhibited by martens in Newfoundland, Canada, and (2) identify the factors influencing use of specific habitats by martens during the winter. A determination of the scale at which martens make movement decisions, and the factors influencing these

movements, provides valuable information for making management decisions, e.g., the design of timber-harvesting plans.

STUDY AREA

I conducted the study in the northwestern portion of the Pine Marten Study Area (PMSA) in Western Newfoundland, Canada. The PMSA is located approximately 50 km southeast of Corner Brook, and was designated in 1972 to try to halt the decline in marten populations on the island. There was no trapping allowed in the PMSA, however, logging operations continued until 1991. My study area (approximately 100 km²) within the PMSA was characterized by a mosaic of first-growth spruce-fir forest interspersed with ponds, bogs, and barrens. Primary tree species included balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*) (Rowe 1972). First-growth stands contained large numbers of uprooted trees and snags. Hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) infestations in the study area have left extensive defoliated stands. The study area also contained 2 clear-cuts, conducted in 1988, that were dominated by broadleaf vegetation. Topography was rugged with elevations ranging from 80-700-m.

METHODS

Marten Tracking

I captured martens in 20 x 20 x 50-cm live traps during the winters of 1990 and 1991. All animals were immobilized with ketamene-hydrochloride (100 mg/ml) weighed, sexed, and fitted with ear tags. If animals were residents, as indicated by recaptures, they were

fitted with radio collars (approx. 21 gm, 1.5-3.8% of body wt.). A total of 8 (4-♂, 4-♀) martens were radio-collared during the study. However, no data were used from 1 female that slipped her collar after 2 days. Following snowfalls, I used a hand-held 3-element Yagi antenna to locate martens, who were then backtracked until trail or light conditions deteriorated. I elected to use snow tracking to identify winter habitat use patterns because it provided more accurate and detailed assessment of habitat use than could be determined using telemetry. At 200m intervals along martens trails I documented locations using an average of 3 readings from a portable Global Positioning System (GPS); GPS error averaged 39.8 m from known points in the study area. In addition, azimuths were sighted forward and backward along visible portions of trails at GPS sampling points.

Habitat Classification

I used multispectral scanner (MSS) satellite imagery with a moderate scale (80m²) to develop habitat cover maps of the study area. The choice of sensor was largely pragmatic; the West Coast of Newfoundland often is obscured by clouds and the only recent (1990) cloud-free image available was from the MSS. Clustering of MSS data into habitat classes was unsupervised. A total of 40 clusters was reduced to 6 classes based on aerial photos, Forestry Canada forest type-maps, ground control points (GCP), and visual evaluation of clusters. I elected to develop a few broad classes because, given a fixed number of samples, there is an inverse relationship between the number of classes and the ability to distinguish selective use of these classes. Validation with an independent group of 126 GCPs (approximately 21 per class), indicated 87.6% agreement between habitat classes and GCPs.

Habitat Selection

I examined the question of marten habitat selection by: (1) comparing the composition of used habitats vs. random samples from the study area, henceforth referred to as landscape-scale selection, (2) comparing the composition of used habitats with surrounding habitats at some minimum scale at which selection could be detected, henceforth referred to as fine-scale selection, and (3) comparing the results of fine and landscape-scale selection. GPS locations from martens trails (200 m intervals) were entered into a geographic information system (GIS) as points, and trails of martens were interpolated by connecting these points with forward and backward azimuths. In the absence of temporal movement data, I assumed that the rate of marten movements was independent of habitat type. Although actual movement rates may vary to some extent, I noted more differences in gait associated with snow conditions, e.g., hard crust vs. new snow, than habitat type. Landscape scale habitat selection was tested by overlaying trails on a classified satellite image, and measuring the amount of each habitat type traversed. The probability of observed marten habitat use occurring by chance was determined by comparing random samples against used trails. Each random sample was composed of 30 transects of 1.18 km with random center points and 1 of 4 randomly assigned orientations (N-S, E-W, NE-SW, SE-NW). Transects were overlaid on the habitat map and classes were tallied. All intersections with non-terrestrial classes, i.e. lakes and rivers, were not used for the analysis and only transects with over 50% of their length overlaying terrestrial habitats were used in the analysis.

To examine the scale at which habitat selection was detectable I constructed

buffers around the 1-pixel-wide trails used by martens in 80-m increments, i.e., the width of 1 pixel, and tested for differences in habitat composition (Fig. 1). Buffers of increasing width were tested in succession until a significant difference in composition was detected. Because the composition of habitats is expected to change as distance increases, a null simulation model

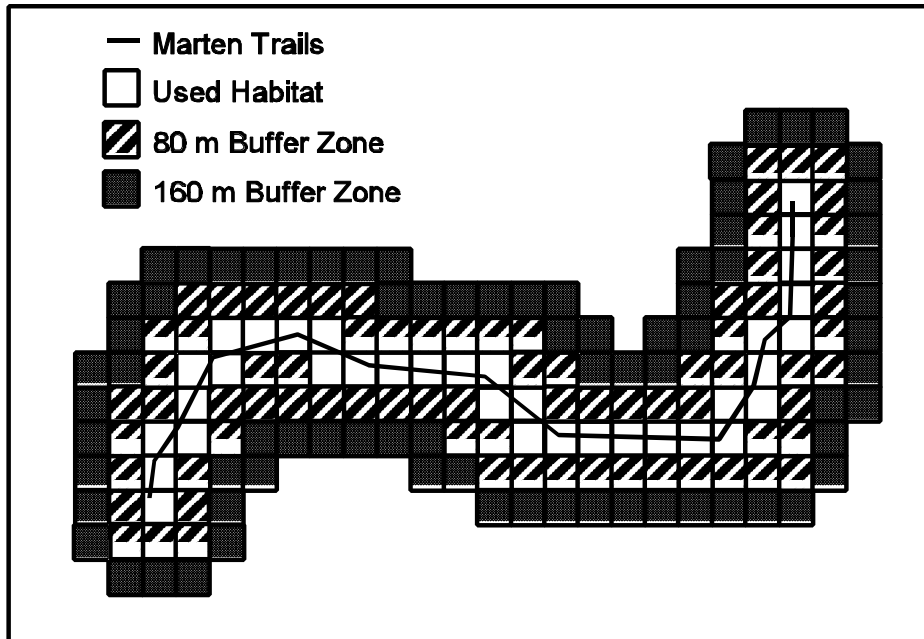


Figure 1. Illustration of the spatial arrangement of cells of the GIS in relation to the trails of martens. The line represents the trail of a marten. Cells with no fill represent "used" habitats. Cells with fills represent habitats included in buffers around used trails.

was used to determine the likelihood of detected differences occurring by chance. Design of this model was similar to the test for study area use. Random transects were overlaid on the study area and buffers were constructed around each transect. If a significant difference was detected between used trails and a buffer of some size, habitat compositions of random transects and buffers of that size were tested to determine the likelihood of this difference by chance. The use of buffers to examine animal-habitat associations is not new. Buffer comparisons are commonly used to with point phenomena, e.g., nest site selection (Hunter et al. 1995, Homer 1991). However, movement paths are not discernable from isolated point data. The use of accurate point locations along contiguous trail segments allowed me to compare used with unused surrounding habitats along the length of the trail.

The distance of buffers from used trails served as a measure of the scale at which martens made their habitat choices. As distance increases, I expect habitat composition to shift from selected habitats towards less desirable habitats. If the movements of martens are based on fine-scale micro-habitat characteristics, e.g., escape cover, then selection should be detectable at a fine scale. Conversely, if the movements of martens are influenced primarily by factors at some larger scale; e.g., clumped distributions of prey, habitat selection should be detected only at substantial distances from used habitats. A limitation on our ability to discern a minimum scale of selection was imposed by the 80 m² resolution of the MSS imagery used to create the habitat cover map. Even if finer scale sensor data such as Thematic Mapper or SPOT had been available, the inability of the

GPS to provide sub-pixel accuracy at 30 m² would have limited detection of finer scale selection.

Statistical Analysis

Comparisons of habitat use between random transects and used trails were made using Chi-square goodness-of-fit test statistics. The null model of random transects was tested against the critical Chi-square value of 11.1 ($\alpha = 0.05$, 5 d.f.). The percentage of random transects with habitat compositions not significantly different from used trails represents the approximate P value. Because use-availability tests have a discrete range (0-100%) with non-normal distributional properties, simultaneous comparisons with confidence intervals are suspect. Instead, significant Chi-square results were interpreted using the standardized residuals for each habitat class. Identification of differences between the habitat composition of buffers and used trails also was based on Chi-square statistics. Habitat compositions of buffers were tested against the expected composition based on used trails. If a significant result was detected, a null simulation was used to test for the probability of random transects having a chi-square statistic greater than or equal to the actual statistic. All tests used an alpha of 0.05.

RESULTS

Landscape Scale Selection

During the winters of 1990-1991 and 1991-1992, I followed 7 martens for a total of 35.45 km in 30 track segments ($\bar{x} = 1.18$, $SD = 1.12$). A comparison between used marten habitats, based on tracking data, and the composition of the study area yielded a

Chi-square value of 37.73. A Monte Carlo simulation indicated that the probability of a sample of transects returning a value equal or higher than the actual statistic was $p = 0.014$ ($n = 500$). Standardized residuals indicate that defoliated and mature conifer stands were used less than would be predicted by chance (Table 1). All other habitats were used less than expected with scrub and regenerating conifer representing the 3rd and 4th largest habitat associations of martens (Koehler and Hornocker 1977, Mech and Rodgers 1977, Cambell 1979, Soutiere 1979, Steventon and Major 1982, Spencer et al. 1983, Bateman 1983). While tracking marten I also noted that they appeared to have core areas of high foraging activity linked by long unidirectional-movements devoid of foraging behavior.

Buffers constructed around the trails of martens suggested a pattern of decreasing selection with increasing buffer size. As buffer distance from trails increased, composition of the greater study area (Fig. 2). This suggests that selection occurred at or below the resolution of our data (80-m cell). Chi-squared statistics comparing habitat composition of used habitat with increasing buffer size indicated that the second buffer (2 pixels;

habitat ($\chi^2 = 63.05$, $P < 0.001$, $d.f. = 4$). As expected, habitats selected by martens had higher proportions of late-seral forest and lower proportions of broadleaf and softwood scrub than the buffers surrounding trails (Table 2). Additionally, habitats used by martens were composed of less immature forest and more defoliated forest than buffers around trails.

Table 1. Partitioned Chi-square residuals comparing winter habitat use of martens in the Little Grand Lake region of Western Newfoundland, during the winters of 1990 and 1991, to null model datasets created from random transects overlaid on the study area GIS.

Habitat Type	Observed (Used Habitats)		Mean Expected (Random Transects ^a)		Mean Standardized Residuals ^a
	N	(%)	N	(%)	
Late-Seral Conifer	112	(52.8)	92.8	(43.8)	0.215
Early-Seral Conifer	8	(3.8)	19.8	(9.3)	0.125
Barrens	18	(8.5)	19.8	(9.4)	0.021
Defoliated	36	(16.9)	18.3	(8.6)	0.369
Scrub	23	(10.9)	39.6	(18.9)	0.195
Broadleaf (Clear-cut)	15	(7.0)	21.3	(10.1)	0.076

^aBased on 500 samples

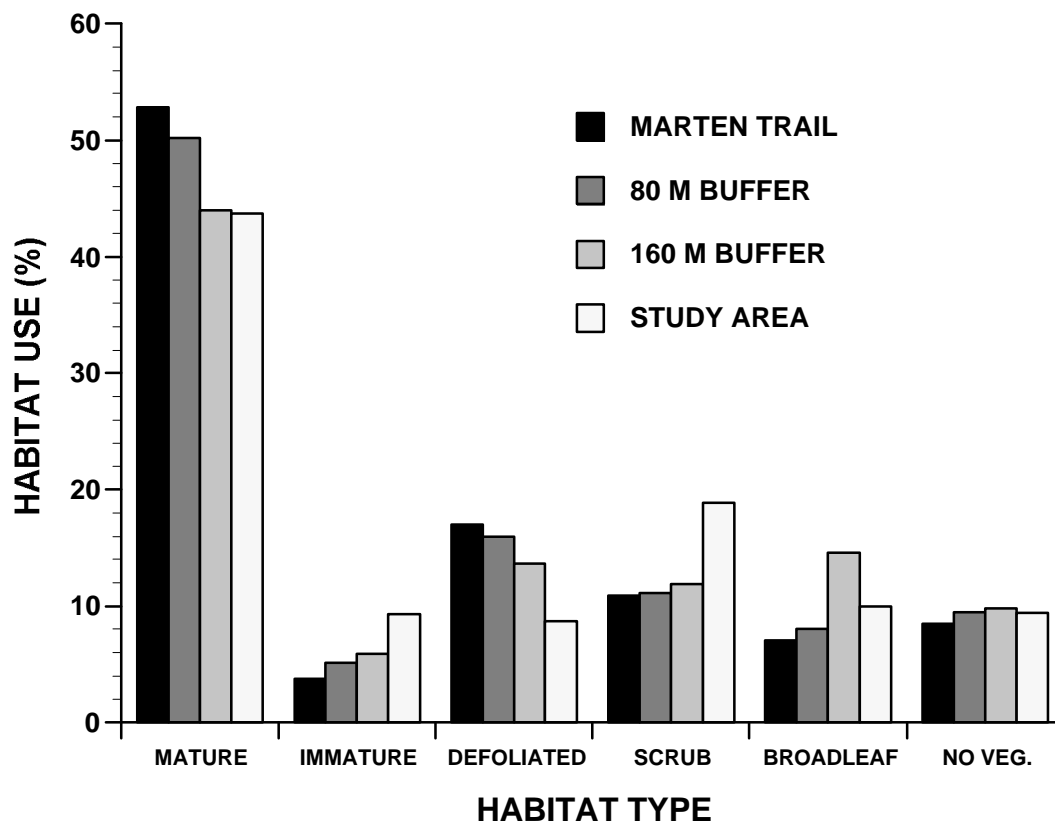


Figure 2. Comparison of the composition of habitats from trails used by martens during the winters of 1990 and 1991, and 80-m buffers, 160-m buffers, and the study area in the Little Grand Lake region of Western Newfoundland.

Table 2. Goodness of fit statistics and standardized χ^2 residuals comparing composition of habitats used by martens in the Little Grand Lake region of Western Newfoundland during the winters of 1990 and 1991 with the composition of 80 m and 160 m buffers around used habitats.

	Observed (80 m Buffer)		Expected (From Marten Trails)		Standardized χ^2 Contribution	Observed (160 m Buffer)		Expected (From Marten Trails)		Standardized χ^2 Contribution
	N	(%)	N	(%)		N	(%)	N	(%)	
≥ Mature Conifer	244	(50.2)	258.8	(52.8)	0.14	238	(44.0)	285.3	(52.8)	0.12
< Mature Conifer	25	(5.1)	18.3	(3.8)	0.53	32	(5.9)	20.4	(3.8)	0.10
Barrens	46	(9.5)	41.3	(8.5)	0.12	53	(9.8)	45.8	(8.5)	0.02
Defoliated	78	(16.0)	82.5	(17.0)	0.06	74	(13.7)	91.7	(17.0)	0.05
Scrub	54	(11.1)	52.7	(10.9)	0.01	64	(11.9)	58.6	(10.9)	0.01
Broadleaf	39	(8.0)	34.4	(7.1)	0.14	79	(14.6)	38.2	(7.1)	0.69
χ^2					4.49 n.s.					63.05 ^a

^a $P < 0.001$, d.f. = 5

n.s.= not significant

DISCUSSION

The integration of satellite derived vegetation maps, accurate mapping of trails, and the GIS analysis tools allowed a highly accurate assessment of habitat selection and a measure of selection scale to the nearest 80 m. At a landscape-scale, martens demonstrated a selection of late-seral conifer forest and a low use of open and early-seral habitats. The extensive use of defoliated forest stands has not been previously reported, though martens in Alaska (Magoun and Vernam 1986) and Wyoming (Sherburne and Bissonette 1993) have shown an ability to use previously forested habitats following fires. The physical structure of forested stands following moderate to low intensity fire events can resemble that left by extensive insect defoliation, and both can provide sufficient resources to make them suitable marten habitat. However, while defoliated forest made up a significant portion of the homeranges of all but 1 marten in Newfoundland, the largest portion of all homeranges was intact mature and older coniferous forest. The use of regenerating clearcuts and deciduous forest on smaller scales in Maine further illustrates that marten habitat selection is a complex decision based on a variety of factors that may be scale dependent (Harrison et al. In Press).

The individual-centered approach to examining habitat use indicated that habitats between 80 m and 160 m from the trail were significantly different from the habitats used by martens. Given the habitat smoothing characteristics of raster satellite imagery, a significant difference could reflect a considerably smaller scale of selection. Marten may discriminate habitats at a scale less than 80 m, however, my ability to detect selection was limited to the resolution of my map and classification scheme. The use of satellite sensors

to map habitats imposes a minimum resolution on the data that may not match the operating scale of a given species or landscape process.

Comparison of landscape- and fine-scale selection of habitats showed agreement with regard to expected use, however, there were some important differences in the magnitude of selection. In particular, the relationship of martens to clearcuts in the study area showed scale dependence. Although slightly less than proportional use of clearcuts was evident at the landscape scale, only at the finer scale of the 2 pixel buffer (80m $x> 160m$) was I able to resolve this distinct lack of habitat use. This discrepancy between coarse and fine scale was likely caused by an interaction between the small proportion of clearcuts in the study area and their location in and around the older conifer stands favored by martens.

The concept of fine-scale habitat selection is intuitively obvious for a foraging animal, however, most of the followed marten trails contained long segments of travel with no hunting behavior. While selection of foraging sites certainly occurs at a fine-scale, my results suggest that even when making non-foraging movements martens in Newfoundland are highly sensitive to surrounding habitats.

MANAGEMENT IMPLICATIONS

While GIS can provide powerful evaluation tools for spatial phenomena, care should be taken to minimize potential errors in interpretation caused by scale dependent relationships. Because selection can be scale dependent, the ecological question being addressed should dictate the appropriate scale. My evaluation of marten movements in

Newfoundland suggest that their habitat selection has a fine scale component apparently not linked to foraging strategies. Some other fine-scale factor, e.g., predation, appears to be influencing marten habitat selection. These results have implications for the design of buffer zones and maintaining continued landscape connectivity. Based on my results it appears that any cutting plan integrating management of martens should avoid any isolation of forest patches. Additionally, based on the scale of habitat selection demonstrated by martens in Newfoundland, landscape linkages less than 160m in width may not be perceived as providing the minimum threshold of habitat quality by martens.

LITERATURE CITED

- Bateman, M. C. 1986. Winter habitat use, habits and homerange size of the marten, Martes americana, in western Newfoundland. *Can. Field-Nat.* 100:58-62.
- Cambell, T. M. 1979. Short-term effects of timber harvests on pine marten ecology. M.S. thesis, Colorado State Univ., Ft. Collins. 71 pp.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Koehler, G. M, and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *J. Wildl. Manage.* 41:500-505.

- Harrison, D., D. M. Phillips, T. G. Chapin, D. P. Katnik, and T. P. Hodgman. In Press.
Pages ---- in G. Proulx, H. Bryant, and P. Woodard, eds. Proc. Second International
Martes Symposium, Provincial Mus. Alberta, Edmondton.
- Homer, C. G. 1991. Modeling sage grouse winter habitat with Landscape Thematic
Mapper data in a Geographic Information System. M.S. thesis Utah State Univ.,
Logan. 28 pp.
- Hunter, J. E., R. J. Gutierrez, and A. B. Franklin. 1995. Habitat configurations around
spotted owl sites in Northwestern California. *Condor* **97**:644-693.
- Magoun, A. J., and D. J. Vernam. 1986. An evaluation of the Bear Creek burn as marten
(Martes americana) habitat in interior Alaska. Bur. Land Management and Alaska
Fish and Game, AK-950-CAH-O. Fairbanks, AK. 58 pp.
- Mech, L. D., and L. L. Rodgers. 1977. Status, distribution and movements of martens in
northeastern Minnesota. USDA For. Serv. Res. Paper NC-143, North Cent. For.
Exp.
Sta., St. Paul, Minn. 7 pp.
- Rowe, J. S. 1972. Forest regions of Canada. Can. For. Ser., Dept. Env. Publ. No. 1300,
172 pp.
- Sherburne, S. S., and J. A. Bissonette 1993. Squirrel middens influence marten (Martes
americana) use of subnivean access points. *Am. Midl. Nat.* 129:204-207.

Snyder, J. E. 1985. The status of pine marten (Martes americana) in western Newfoundland.

Unpubl. Rep. Prepared for COSEWIC. St. John's, Newfoundland.

_____, and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in

western Newfoundland. *Can. J. Zool.* 65:169-174.

Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. *J. Wildl. Manage.*

43:850-860.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the

northern Sierra Nevada. *J. Wildl. Manage.* 47:1181-1186.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut

forest. *J. Wildl. Manage.* 46:175-182.

CHAPTER III²**WINTER ACTIVITY PATTERNS OF AMERICAN MARTEN (*Martes americana*) IN
NEWFOUNDLAND³****Abstract**

Previous studies on winter activity patterns of marten have yielded conflicting results regarding the daily activity patterns of American marten. Despite their temperate to sub-arctic geographic range, American marten possess a thermally inefficient morphology. The lack of morphological adaptations for reducing thermal costs suggests that marten may use behavioral strategies to optimize thermal budgets. During the winters of 1989-1990 and 1990-1991, I radio-collared and monitored diel activity of 7 marten. A regression of the percent active fixes on ambient temperature had a negative slope ($b = -4.45$, $p = 0.084$, $n = 12$); the opposite of what a thermal optimization strategy would predict. A log-linear model suggested that the presence or absence of light was the only factor associated with marten activity patterns ($p < 0.001$). Contents of marten scats suggested that marten were not synchronizing their activity patterns with that of their major prey items. While martens must balance multiple life requisites, their activity patterns fail to support the influence of either temperature or prey availability considerations. The nocturnal habits of Newfoundland martens in the winter were consistent with the avoidance of predation risk hypothesis.

²Canadian Field-Naturalist Format.

³Co-authored with J. A. Bissonette

Introduction

Animals living in thermally stressful environments typically acquire morphological, physiological, or behavioral adaptations to assist in thermal regulation (Chappell 1980). However, American martens (Martes americana), like other small mustelids, do not appear to possess significant morphological or physiological adaptations for thermal efficiency (Brown and Lasiewski 1972, Buskirk et al. 1988). The morphological characteristics of martens suggest a tradeoff between thermal efficiency and predatory efficiency, i.e., a long thin body, minimal body fat reserves, and a short pelage allow them to enter confined spaces in search of small prey (Brown and Lasiewski 1972, Buskirk et al. 1988). However, these adaptations exact a high toll in homeothermic efficiency (Schmidt-Nielson 1983, Brown and Lasiewski 1972). Laboratory studies have found the minimum critical temperature (MCT) of marten to be in the range 16°C (Buskirk et al. 1988, Adair and Bissonette, 1995 Utah State Univ., unpubl. data) to 29°C (Worthen and Kilgore 1981). Below the MCT, marten at rest must increase their metabolic rate to compensate for heat loss. Based on these constraints, marten might be expected to minimize their exposure to low temperatures, particularly during the winter months. Marten in Wyoming (Buskirk et al. 1988) and Alaska (Buskirk 1984) selectively used thermally efficient resting sites during the winter. These results are consistent with the hypothesis that marten have developed behavioral adaptations for maintaining thermal homeostasis.

In addition to using thermally efficient resting sites martens could also decrease thermal costs through limiting activity during the colder portions of the day. However, variability in the winter activity patterns of American marten suggest that the timing of

marten activity is based on multiple factors. Martens in Alberta (More 1978), and Ontario (Thompson and Colgan 1994) were found to be diurnal during the winter apparently in an attempt to limit homeothermic costs. In contrast, Zelinski *et al.* (1983) and Martin (1987) found marten in California to be primarily nocturnal during the winter. Zelinski *et al.* (1983) suggested that the adoption of nocturnal activity patterns during winter could be a result of the synchronization of marten activity with that of their prey during the period when prey are less detectable due to snow cover. One point of general agreement is that the total time spent active is lower during the winter (Zelinski *et al.* 1983, More 1978).

The purpose of this study was to examine the activity patterns of marten in Newfoundland during the winter to test whether martens minimize their exposure to the coldest temperatures (i.e., marten activity decreases with decreasing ambient temperature). If martens failed to minimize their thermal costs behaviorally, I wanted to examine the possible causes for their thermally inefficient behavior. Other hypotheses that might influence the temporal activity patterns of martens are: (1) activity of martens may be synchronized with that of their prey to increase foraging success, or (2) martens may be limiting their activity to times when predation risk is lowest. I addressed the first alternative hypothesis by examining the activity patterns of prey species detected in the scats of martens. If the activity patterns of martens are a result of attempts to synchronize activity with that of their prey items, their primary prey should be nocturnal. Data on predator density and activity was limited, so assessment of the second alternative hypothesis was limited and inferential.

Methods

This study was conducted in the northwestern portion of the Pine Marten Study Area (PMSA) in Western Newfoundland, Canada (Bissonette et al. 1988). The PMSA, located approximately 50 km south of Corner Brook, was set aside in 1972 to arrest the decline in marten populations on the island. Although there is no mammal trapping allowed in the PMSA, logging operations continued until 1991. The study area is characterized by a mosaic of old growth forest interspersed with ponds, bogs, and barrens. Primary tree species include balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*) (Snyder and Bissonette 1987). Old growth stands contained large numbers of uprooted trees and snags. Hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) infestations in the study area have left large defoliated stands. Topography is rugged with elevations ranging from 80-700 m (Snyder and Bissonette 1987, Bissonette et al. 1988).

A total of 8 marten (4 ♀: 4 ♂) were captured in 20 x 20 x 50-cm live traps during the winters of 1989-1991. Animals were immobilized with ketamene-hydrochloride (100 mg/ml). All marten were fitted with radio-collars (approx. 21 g). However, no data were used from 1 female that slipped her collar after 2 days. Martens activity was treated as a dicotomous variable; either active or not. Activity was determined by evaluating the telemetry signal variation. Signals with erratic strength and pitch indicated active animals (Sunquist and Montgomery 1973, Zelinski et al. 1983). These measurements were taken during daily telemetry relocations and during activity monitoring sessions conducted at all hours of the day and night. Observations were separated by a minimum of 30 minutes and

grouped into 2 hr blocks, following the protocol of Zelinski et al. (1983). The percentage of fixes within each 2 hour block were calculated and used as a representation of the activity level of the 7 monitored martens. I tested for an dependency of marten activity level on temperature with a regression analysis. A significant result with a positive slope would support the hypothesis that martens are primarily constrained by thermal constraints. Conversely, a lack of correlation, or a slope other than positive, would indicate that martens were trading-off thermal efficiency for some other factor. Log-linear models were used to test for variation in marten activity due to: individuals ($n = 7$), age-class ($n = 2$), sex ($n = 2$), and presence or absence of light ($n = 2$). Temperature was not included in the log-linear models because of the obvious covariance with light, and its previous testing in the regression analysis.

To determine the predatory habits of martens, I collected scats encountered while snow tracking radio-collared martens. In addition, I was able to draw on a marten diet study conducted in our study area during the winter of 1986-1987 (Tucker 1988). The frequency of occurrence of prey in scats was used to quantify marten diet components so my results could be compared to the previous study. The determination of marten predators included direct observation, tracks, and a raptor call count in the winter of 1990-1991.

Results

Marten Activity

A total of 273 activity measurements were made on 7 telemetered marten from January-March of 1989 and 1990. Within each 2 hour block an average of 23 measurements were made. Activity patterns during these winters were predominantly nocturnal (Fig. 1). The

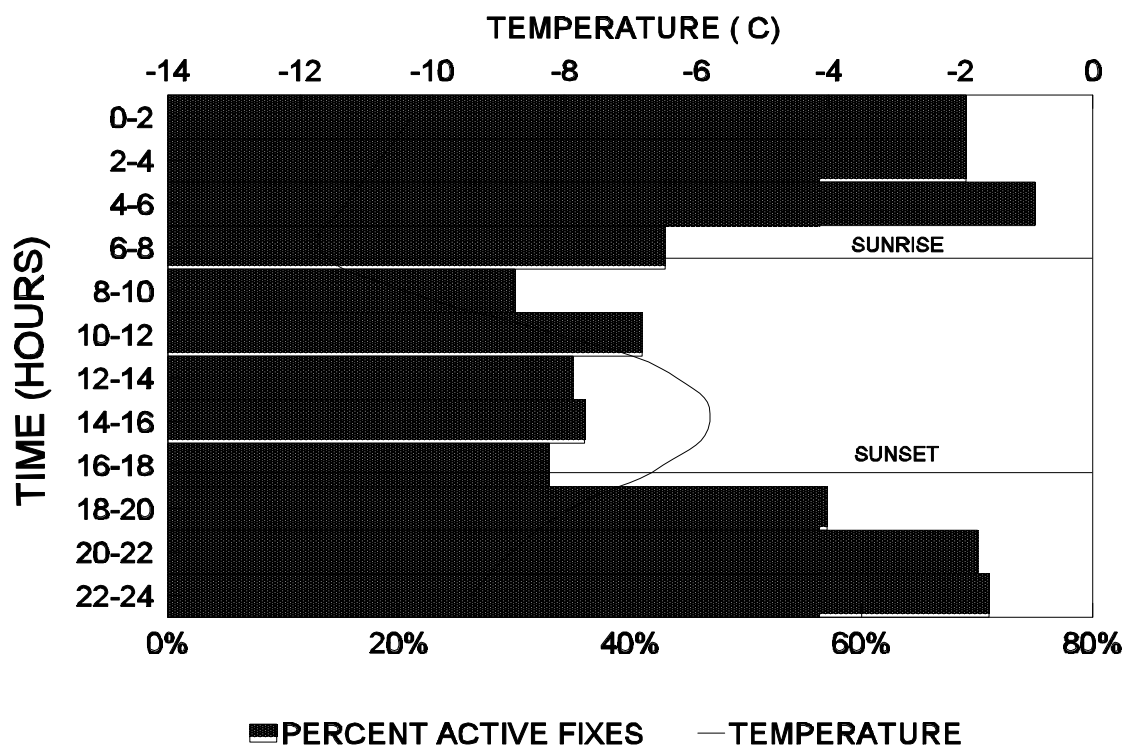


Fig. 1. Diel activity patterns of martens at Little Grand Lake, Newfoundland during the winters of 1989-1990 and 1990-1991. The line represents mean temperatures over the diel period. Bars indicate average activity levels of marten. Bold horizontal lines represent average sunrise and sunset over the sampling period.

regression of mean activity level on temperature for each 2 hour sampling-block was not significant ($P = 0.084$). However, a negative slope ($b = -4.45$), indicated that marten activity varied inversely with temperature, i.e. marten activity increased as temperature decreased. The plot of marten activity over the diel period illustrates that the presence or absence of light appeared to explain the general pattern of marten activity (Fig. 1). This was supported by the best fit log-linear model (Light)(Table 1). Marten activity levels were significantly lower during the daylight hours than at night. This result also could explain the inverse relationship between marten activity and ambient temperatures, i.e., temperature is dependent on solar insolation. Although the number of martens monitored was small (7), a log-linear model failed to detect any significant variation in activity patterns by individuals (Light)(Activity)(Individual) (Table 1). Neither sex or age were found to be significant factors, although juveniles and males did display slightly higher activity rates than adults and females respectively.

Marten Diets

The diets of martens throughout North America tend to be similar, with local microtines providing the bulk of marten diets in Alaska (Buskirk and MacDonald 1984), Maine (Soutiere 1979), Montana (Weckwerth and Hawley 1962), Newfoundland (Tucker 1988), the Northwest Territories (Douglass *et al.* 1983), and Utah (T. Hargis, Utah State University, pers. commun.). However, to be sure that martens in the study area followed this pattern I collected scats from the martens I tracked. The small number of scats

examined (12) precluded statistical analysis. However, since all scats were collected from trails of known marten, they

Table 1. Results of G-tests to examine potential causes for the activity patterns of marten in the Little Grand Lake area of Newfoundland during the winters of 1989-90 and 1990-91.

Model	d.f.	Parameter Estimates	G-value
(Age)	1	0.49	0.47
(Light)	1	***	25.60
(Sex)	1	0.19	1.71
(Age)(Light)	1	0.69	0.16
(Sex)(Light)	1	0.63	0.21
(Individual)(Light)	6	0.46	5.70

*** $P < 0.001$

gave an indication of prey consumed by the monitored marten (Table 2). I also had the benefit of data from a previous diet study in the area during 1985-1986. The relative agreement between my sample of scats and that collected by Tucker (1988) gave me confidence in concluding that the most common component of marten diets in the study area was Microtus pennsylvanicus. During my study the only known mortality was attributable to predation by a red fox. Previous research in the same study area, recorded 3 mortalities attributed to predation (Bissonette et al. 1988).

Discussion

Because martens do not appear to possess significant morphological or physiological adaptations for thermal efficiency they must regulate their thermal costs through primarily behavioral means. The selection and use of thermally efficient subnivean resting sites by martens indicates that martens do take advantage of available thermal protection (Buskirk et al. 1989). However, because the thermal benefits of subnivean resting sites are dependent on ambient temperature, i.e. as temperature decreases potential benefits increase, maximum thermal benefit would be accrued by resting during the coldest portions of the day. Chappell (1980) estimated that arctic animals, including ermine (Mustela erminea), could save an average of 30% of their thermoregulatory costs by leaving burrows only on sunny days. Hence, during the winter, when martens are faced with high thermodynamic costs, they could substantially decrease thermal maintenance costs by using subnivean resting points during the night and confining activity to daylight hours.

Table 2. Activity patterns of marten prey items present in the Little Grand Lake area of Western Newfoundland and the frequency of occurrence of prey items in scats collected during the winters of 1986-1987 and 1990-1991.

Species	Winter Activity Patterns	Occurrence in Scats (%)	
		1990-1991(n=12)	1986-1987 (n=30) ¹
<u>Lepus americana</u>	Nocturnal ²	8.3	3.3
<u>Microtus pennsylvanicus</u>	All Times ³	50	66.7
<u>Peromyscus maniculatus</u>	Diurnal	0	-
<u>Sorex cinereus</u>	All Times ²	16.7	23
<u>Tamiasciurus hudsonicus</u>	Diurnal ²	16.7	20
Birds	Diurnal	33.3	10.5
Carrion	None	8.3	0.1
Vegetation	None	33.3	13.3

¹Tucker 1988, ²Banfield, A. W. F. 1974, ³Madison 1984.

However, my data, as well as the studies conducted in California (Zelinski et al. 1983, Martin 1987), indicate a pattern of primarily nocturnal activity during the winter months. While this is at odds with More's (1987) study in Alberta, and Thompson and Colgan's (1994) study in Ontario, climatological data indicate mean ambient temperatures for January are lower in both More's and Thompson and Colgan's study areas in central Canada (-17.5°C) than marten study areas in either California (0°C) or Newfoundland (-7.5°C) (WMO 1979). These differences suggest a possible temperature threshold at higher latitudes and altitudes, where thermal constraints may take precedence over other factors influencing marten activity patterns. My data show that martens in Newfoundland, which is characterized by less extreme winter temperatures, fail to limit thermal costs through their diel activity patterns.

Zelinski, et al. (1983) suggested that the thermally inefficient activity patterns of martens they studied in California could be related to a strategy to increase hunting efficiency by synchronizing their activity patterns with those of their primary prey species. This hypothesis would seem to require that a major portion of marten diets be composed of species with nocturnal activity patterns similar to those of martens. A literature review of the prey species available to martens on the island indicates that the majority of marten prey are not nocturnal during winter. The most common prey species from both my minimal scat analysis, as well as the previous food habits study conducted in the study area (Tucker 1988), tend to be active at all times of day; meadow vole (*M. pennsylvanicus*); red squirrel (*Tamiasciurus hudsonicus*) (Table 2). The only prey species known to exhibit nocturnal activity patterns in the study area were snowshoe hare (*Lepus americanus*) and deer mice (*Peromyscus maniculatus*), neither of which were a common constituent in either scat analysis conducted on the study area. While there was no evidence for

synchronization of activity patterns of prey, when captured to remove radio-collars in early spring martens showed appeared to be in good physical condition with only minor drops in body-weight from over the test period. Even without any obvious synchronization with prey, martens were able to survive on available forage.

An alternative to any of the previous hypotheses is that martens might rest during the warmer portions of the day and hunt during the coldest to take greatest advantage of the substantial heat released through physical activity, i.e. hunting. However, such a strategy would require substantial prey resources that were not available in the study area (Bissonette et al. 1988). In fact, the low numbers of prey and prey species has been cited as a major factor limiting recovery of the Newfoundland marten populations (Bissonette et al. 1988).

My evidence does not provide a definitive explanation for why marten in Newfoundland and California are nocturnal during the winter months. However, given that marten in these areas are sustaining substantially increased thermal costs, the ultimate costs of not assuming nocturnal winter activity patterns must be greater. A potential alternative explanation is that because marten are relatively long-lived and late in reaching sexual maturity they may try to limit their own exposure to predation by being active when predators are less efficient. I suggest that low-light conditions would have less effect on the hunting patterns of marten, which are predominantly subnivian, than on the efficiency of potential supernivian marten predators such as red fox.

The disagreement between studies suggests 2 important points. First, martens appear to be behaviorally plastic in their activity patterns. The environmental constraints placed upon martens may limit them to a narrow range of responses and preclude any stereotypical activity pattern. Secondly, these behaviors are likely dependent on a combination of factors including: (1)

minimizing energetic costs (2) energy acquisition, and (3) avoiding mortality risks. Detailed research on the tradeoffs between these factors will be necessary to better understand the decision making processes of marten.

Literature Cited

- Banfield, A. W. F. 1974. The mammals of Canada. National Museum of Natural Sciences. University of Toronto Press. 438 pp.
- Bissonette J. A., R. J. Fredrickson, and B. J. Tucker,. 1988. The effects of forest harvesting on marten and small mammals in western Newfoundland. Report prepared for the Newfoundland and Labrador Wildlife Division, and Corner Brook Pulp and Paper Company, Limited. Utah Cooperative Fish and Wildlife Research Unit, Utah State Univ., Logan, UT. 108 pp.
- Brown, J. H., and R. C. Lasiewski. 1972. Metabolism of weasels: The cost of being long and thin. *Ecology*. **53**:939-943.
- Buskirk, S. W., 1984. Seasonal use of resting sites by marten in South-Central Alaska. *J. Wildl. Manage.* **48**:950-953.
- _____, and S. O. Macdonald. 1984. Seasonal food habits of marten in south-central Alaska. *Can. J. Zool.* **62**:944-950.
- _____, H. J. Harlow, and S. C. Forrest. 1988. Temperature regulation in American marten (*Martes americana*) in winter. *Nat. Geog. Res.* **4**:208-218.

- _____, S. C. Forrest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting ecology of marten in the central Rocky Mountains. *J. Wildl. Manage.* **53**:191-196.
- Chappell, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic animals. *J. Mammal.* **61**:278-291.
- Douglass, R.J., L.G. Fisher, and M. Mair, 1983. Habitat selection and food habits of marten *Martes americana*, in the Northwest Territories. *Can. Field Nat.* **97**:71-74.
- Madison, D. M. 1984. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. Pages 267-274 in J. F. Merritt ed. Winter ecology of small mammals. Special Pub. of the Carnegie Museum of Natural History No. 10. 380 pp.
- Martin, S. K. 1987. The ecology of the pine marten (*Martes americana*) at Sagehen Creek, California. Ph.D. Dissert. Univ. California, Berkeley. 223 pp.
- More, G. 1978. Ecological aspects of food selection in pine marten. M.S. thesis, University of Alberta, Edmonton. 94 pp.
- Murie, A. 1961. Some food habits of the marten. *J. Mammal.* **42**:516-521.
- Pulliainen, E. 1981. Winter habitat selection, home range, and movements of the pine marten, *Martes martes* in a Finnish Lapland forest. Pages 1068-1087 in J. A. Chapman and D. Porsley eds. Proceedings of the Worldwide Furbearer Conference, Frostburg, MD. R. R. Donnelley and Sons Company, Falls Church, Virginia.

- Schmidt-Nielson, K. 1983. *Animal physiology: adaptation and environment*. Cambridge Univ. Press, N.Y. 181 pp.
- Sherburne, S. S., and J. A. Bissonette 1993. Squirrel middens influence marten (Martes americana) use of subnivean access points. *Am Midl. Nat.* 129:204-207.
- Snyder, J. E., and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. *Can. J. Zool.* 65:169-174.
- Soutiere, E. C. 1978. Effects of timber harvesting on marten in Maine. *J. Wildl. Manage.* 43:850-860.
- Sunquist, M. E., and G. G. Montgomery. 1973. Activity patterns and rates of movement of two-toed and three-toed sloths (Choloepus hoffmani and Bradypus infuscatus). *J. Mammal.* 54:946-954.
- Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. *J. Wildl. Manage.* 58:280-288.
- Tucker, B. J. 1988. The effects of forest harvesting on small mammals in western Newfoundland and its significance to marten. M.S. thesis, Utah State University, Logan, Utah. 52 pp.
- Weckwerth, R. P., and V. D. Hawley. 1962. Marten food habits and population fluctuations in Montana. *J. Wildl. Manage.* 26:55-74.

Worthen, G. L. and D. L. Kilgore. 1981. Metabolic rate of pine marten in relation to air temperature. *J. Mammal.* **62**:624-628.

Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. *J. Mammal.* **64**:387-396.

CHAPTER IV⁴

PERCEPTION OF RISK BY AMERICAN MARTEN (Martes americana): INFLUENCES OF HABITAT AND PREDATOR CUES⁵

ABSTRACT

American marten (Martes americana) appear to be habitat specialists, using primarily late-seral conifer forest, however, potential causes for this association have not been tested experimentally. Experiments conducted on marten in Newfoundland, Canada; Yellowstone National Park, Wyoming; and Utah were used to test for their responses to habitat and predator cues. Although the limitation of marten to late-seral forest habitats has been linked to requirements for access to subnivean prey and thermally advantageous resting sites, the risk of predation could also help account for the association of marten with these habitats. In field experiments, martens in Newfoundland and Yellowstone National Park, Wyoming were offered food resources at various distances from the edge of 3 habitat types, providing martens with a spectrum of habitat cues while holding food resources constant. Rates of visitation by martens at bait-boxes did not differ by study site or between late-seral and defoliated habitats. Martens did use bait-boxes in defoliated habitats more than boxes in habitats lacking both foliation and stem structure. Captive experiments indicated that martens from Utah selected areas possessing both overhead cover and woody stem structure. No difference was detected between the use of areas possessing only overhead cover and those possessing only stem structure, though the size of the pen may have limited the ability to

⁴Animal Behavior format.

⁵Co-authored with John A. Bissonette

make this comparison. Martens decreased foraging effort regardless of habitat when presented with predatory cues. These experiments show that martens are sensitive to predation threats and that these perceived threats can influence their habitat use.

Habitat use is often a compromise between requirements for food, shelter, and security from predation. However, because of the asymmetrically high costs of predation when compared to requirements for food or shelter, all but short-lived species should have a low tolerance for predation risk (Bouskila and Blumstein 1992). Organisms can decrease risk by restricting activities to habitats or times that limit the efficiency of predators, however, there often are costs associated with access to resources (Sih 1980). The avoidance or limitation of activity in certain habitats has been documented for fish (Werner et al. 1983), birds (Caraco 1980), and rodents (Kotler 1984). Organisms can use habitats to decrease encounters or increase chances of escape (Lima and Dill 1990). Adaptations permitting habitat specialists to persist can disadvantage them when new species are introduced and/or disturbances occur (Seal et al. 1989). These problems are especially acute for carnivores, e.g., American marten (*Martes americana*), that occur in relatively low densities (Buskirk and McDonald 1989).

Numerous studies have shown a pattern of close association between marten and coniferous forests containing large trees and abundant coarse woody debris (CWD), henceforth referred to as coniferous forest (Koehler and Hornocker 1977, Mech and Rodgers 1977, Cambell 1979, Soutiere 1979, Steventon and Major 1982, Douglass et al. 1983, Spencer et al. 1983, Zielinski et al. 1983, Snyder and Bissonette 1987). The loss of coniferous forest types has been recognized as the major factor leading to the reduction in numbers or extirpation of marten in parts of North America

(Davis 1983, Thompson 1991). However, debate remains over the mechanisms responsible for decreases in marten populations. The affinity of martens for coniferous forest is commonly attributed to seasonal limitations on access to prey (Koehler and Hornocker 1977, Francis and Stephenson 1972) or thermally advantageous resting sites (Buskirk et al. 1989, Buskirk 1984). During the winter months, access to the subnivean zone is limited by the physical structure of the forest. Given that martens occur in northern coniferous forests characterized by high snowfall, access to prey could potentially constrain marten habitat choice. However, research in Yellowstone National Park found that martens use of subnivean access points was related to prey biomass; subnivean access points were not limiting (Sherburne and Bissonette 1994). Additionally, several researchers have suggested that martens are susceptible to predation, however, none have experimentally tested this hypothesis (Thompson and Colgan 1994, Thompson 1991, Herman and Fuller 1974).

Avoidance of high risk areas has been demonstrated in numerous species, including bluegill sunfish (Werner et al. 1983), heteromyid rodents (Brown et al. 1988), and moose (Edwards 1983). Habitat structures often are used to moderate predation risk or the perception of risk (Sih 1980, Edwards 1983, Werner et al. 1983). Coniferous forests provide 2 conspicuous physical components that may be perceived by martens as security or escape cover, (1) foliar cover, which provides concealment, and (2) coarse woody stem structure, i.e., live stems, snags, and coarse woody debris, which provide escape routes. However, since foliar cover and stem structure tend to be covariates, their independent influence on marten habitat use is poorly understood.

Dense foliar canopies, common in coniferous forest stands, may provide martens with required cover from avian predators (Hargis and McCullough 1984, Pulliainen 1981, Hawley and Newby

1957), and could be especially important during the winter months, when their dark brown winter pelage contrasts with snow cover. Although there is limited evidence of avian predation on American marten, in Finland, golden eagles (Aquila chrysaetos) are known to prey upon pine marten (M. martes)(Nyholm 1970, Pulliainen 1981). Additionally, attacks on martens have been recorded in Newfoundland, Canada by hawk owl (Surnia ulula) (Bissonette et al. 1988) and in California by prairie falcon (Falco mexicanus)(Murie 1961).

Stem structure also has been linked to marten refuge. The stereotypical practice of climbing trees to escape potential predators (Raine 1982, Pulliainen 1981) may explain early anecdotal accounts of marten as primarily arboreal. This view was generally accepted until researchers, who were snow tracking martens, determined that marten movements were almost exclusively terrestrial (Hawley and Newby 1957, de Vos 1952).

This research had 2 primary objectives: (1) I wanted to determine whether habitat cues influenced perceived predation risk, and (2) I wanted to identify which cues influenced this perception. These questions were addressed with a series of pen and field experiments. The Prior to this study, the role of stem structure and foliation as cues for marten perception of predation risk had not received systematic examination. Designing and conducting manipulation experiments for mobile species at scales sufficient to resolve causal mechanisms are difficult (Wiens et al. 1986). However, the ability of this approach to directly test hypotheses explaining the obligate use of coniferous forest habitats by martens made it essential.

METHODS

Study Areas

My first study area was located within the Pine Marten Study Area (PMSA) of western Newfoundland, Canada, approximately 50 km south of Corner Brook. The PMSA (approximately 1600 km²) was designated in 1972 as a reserve where martens could be studied in an effort try and halt the population decline in marten on the island. During the winter, temperatures in the area typically range from approximately 12°C to -38°C. All trapping was prohibited in the area, however, logging operations continued in the PMSA until 1991. The area is characterized by a mosaic of coniferous forest interspersed with ponds, bogs, and barrens. Primary tree species include balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*)(Rowe 1959). Forest stands contain large numbers of uprooted trees and snags. Infestations of hemlock looper (*Lambdina fuscicollis*) and spruce budworm (*Choristoneura fumiferana*) have left large defoliated stands. Topography is rugged with elevations ranging from 80-700m. While large portions of the PMSA had been harvested, less than 4% of the forest in my study area had been cut.

My second study area was the Canyon-Norris region of Yellowstone National Park (YNP) which had a healthy and stable marten population. The dominant common cover type in the area was lodgepole pine (*Pinus contorta*). The matrix of lodgepole pine also contained moderate to small interspersions of engelman spruce (*Picea engelmannii*) and douglas fir (*Pseudotsuga menziesii*) stands. Elevations in the study area ranged from 2500-3500 m. During the winter, temperatures in the area ranged from 5°C to -60°C. The 1988 fires left large areas of standing dead trees. Though defoliated stands in Yellowstone were caused by fire, they provided structural characteristics similar to insect killed stands in Newfoundland.

Captive trials were conducted during the summer of 1993 at the Utah State University Green Canyon compound in Logan, Utah. Martens were captured in the Uinta mountains wilderness area in eastern Utah and transported to holding pens (800 cm x 300 cm x 300 cm) at the Green Canyon compound for the duration of the study.

Field Experiments

I developed a field experiment to partition the influences of foliar cover and stem structure on perceived risk by marten during the winter. Martens were offered food in each of 3 habitat types, (1) coniferous forest (stem structure and foliage), (2) defoliated (only stem structure), and (3) open (no structure or foliage) within each marten home-range. Bait-boxes were constructed of plywood (60 cm x 40 cm x 25 cm) with a 7.5 cm circular entrance that restricted access of non-targets to the bait. Baits consisted of 60 gm pre-packaged patties of commercial dog food. A single box was baited and scented with commercial skunk lure near a habitat edge until discovered by a resident marten. Bait was checked daily, and following discovery and consumption, it was replaced as needed for 3 days before beginning the experiment. Trials consisted of placing 3 resource boxes at 3 intervals, 25, 50, and 75 m, first, from a habitat edge into coniferous forest, then defoliated, and finally into habitats devoid of cover. Trials were run for 3 days in each habitat, checking bait-boxes daily for visitation and replacing bait as needed. Additionally, I measured overhead cover at bait-box locations with a semi-hemispherical densiometer, and tallied the number of stems >10 cm DBH within a 5 m radius around bait-boxes. These measurements gave me specific micro-habitat information from which study sites and habitat types could be compared independent of my habitat classifications, i.e., open, defoliated, and coniferous. Each

animal was presented with bait-boxes in the same order, from most to least structure. The sequence of presentation was important for 3 reasons. First, it controlled for variances between marten responses based on order of presentation. This was important because of the anticipated small sample size. Secondly, the sequence allowed us to isolate the effects of foliar cover, and had the potential to isolate complex stem structure if foliar cover turned out to be unimportant. Finally, the sequence also allowed martens to gain experience with the boxes in habitats with the greatest cover before being placed in less commonly used habitat types. Thus biases caused by differential encounter rates among tested habitats and potential confusion caused by missing contextual cues; e.g., stems, was minimized.

For these experiments to be valid, each trial had to be independent. Although martens are known to have intra-sexually exclusive home-ranges (Hawley and Newby 1957, Francis and Stephenson 1972, Bissonette et al. 1988), overlapping intersexual home-ranges meant that home-range alone was not sufficient to ensure independence. To identify areas of exclusive use in Newfoundland during the winter of 1989-1990., I trapped and fitted 4 martens with radio collars and used telemetry locations to identify their home ranges. Areas of exclusive use were then identified using home-range maps. Within areas of exclusive use, test subjects had to have sufficiently large (150 m diameter) contiguous blocks of coniferous, defoliated, and open habitats types. Only 2 marten in Newfoundland met all of these criteria. Data was also collected on a third marten for coniferous and open habitats.

In YNP I relied on marten telemetry data collected the previous summer by Sherburne (1992). I identified 4 marten that met my qualifications, however, 1 marten was apparently not present at the time of my trials. This gave independent field tests of 6 martens (3 from Newfoundland and 3

from Yellowstone N.P.). Prior to testing for differences due to habitats I compared visitation rates for study sites and individuals to identify potentially confounding sources of variation. I used randomization tests for the first 3 test questions due to their statistical power when testing non-normal distributions of data commonly encountered when sample sizes are limited.

Study site differences

I first tested for differences due to study site by comparing marten visitation rates at bait-boxes using the equation (Noreen 1989):

$$\underline{S} = *(\bar{O}_x/n_x) - (\bar{O}_y/n_y)* \quad (1)$$

where \underline{S} is the test statistic based on the absolute value of differences between mean study site visitation rates, x and y are samples of visitation rates for the 2 study sites, and n_x and n_y are the numbers of samples from each study site. For example if the actual test statistic were $*125/5 - 20/5* = 21$, and in 100 random samples, 3 samples were greater than or equal to 21, the probability of this arrangement of samples by chance would be approximately 0.03.

Individual differences.

To identify differences due to individual visitation rates at bait-boxes I used the equation (adapted from Noreen 1989):

$$\underline{S} = \underline{O}^*(x_i) - \underline{Y}^* \quad (2)$$

where \underline{S} is the test statistic based on the absolute value of variance from the actual visitation rate, x_i is the mean visitation rate across all habitat types and distances for animal I, and \underline{Y} is the mean visitation rate for all animals.

Habitat use.

My first question, "Do marten perceive different habitats as conferring different levels of predation risk?" was tested using a randomization test. The equation used to generate a test statistic was the same as equation (2), however, for this test x_i was the sum of visitation rates for the i^{th} habitat type, and n_i was the sample size in the i^{th} habitat. If marten do perceive differences in risk of predation between habitats, I should see significantly different visitation rates at bait-boxes in different habitat types. The null hypothesis tested was H_0 : visitation rates at bait-boxes in different habitats are not different.

Foliar cover

If H_0 is rejected, I could ask the question; do marten perceived the presence of foliar cover as decreasing exposure to predation risk? I tested this second question by comparing marten visitation rates at bait-boxes in coniferous and defoliated forest using a Tukey multiple comparison test. If marten perceive a decreased risk of predation in stands with foliar cover, I should see significantly lower visitation rates of bait-boxes in defoliated stands due to the lack of

foliar cover. The null hypothesis tested was H_02 : visitation rates at bait-boxes in coniferous or defoliated forest are not different. If H_02 was rejected I would conclude that foliar cover is important to marten as cover from predation.

Stem structure

I was also interested in whether marten perceive the presence of stem structure as decreasing predation risk. I tested this question by comparing marten visitation rates at bait-boxes in defoliated stands and clearings using a Tukey multiple comparison test. If marten perceive a decreased risk of predation due to the presence of stem structure, I should see significantly lower visitation rates of bait-boxes in clearings due to the lack of stem structure. The null hypothesis tested was H_03 : visitation rates at bait-boxes in defoliated forest with rates in open areas are not different.

In addition to recording visitations at boxes, I made detailed diagrams of marten tracks around bait-boxes for each exposure day. I used these diagrams to qualitatively evaluate marten use of bait-boxes and to quantitatively measure any boundary effect in relation to habitat edge.

Captive Experiments

Arena design

A 10 m x 13 m x 2.2 m pen served as the trial arena. Plastic tarps were used to simulate canopy cover. Stem structure was created using 2 to 4 m lengths of lodgepole pine 25 to 40 cm diameter. Because of the relatively small size of the trial arena, I limited tests to simple dichotomous choices. Commercial cat food was used for marten daily rations as well as for baits in trials. Martens were put on half rations the day prior to testing to assure that they would

show interest in baits. Kernels of cat food ($n = 30$) were mixed with 6 L of millet and the combination placed in a plastic tray (60 cm x 40 cm). For each trial, 1 tray was placed in the center of the northern half of the arena, and 1 tray was placed in the center of the southern half of the arena. Holding cages were fitted with 10 cm circular gates. A flexible 10 cm diameter tube provided access to the trial arena. Martens were released into the trial arena by remotely operating the circular gates. As martens removed pieces of bait, the remaining pieces became more difficult to locate in the millet, making it more likely that foraging differences would be detected. I recorded all trials with 2 VHS cameras, providing a permanent record of the trials and eliminating the potential for bias due to detection of observers during trials. Before beginning trials, each marten was introduced to the trial arena once for approximately 5 minutes to habituate them to release and recovery procedures. All work was done in accordance with Utah State University guidelines regarding care and treatment of animal subjects.

Design of trials

A total of 5 martens were tested in captive trials. To identify any cage effects, every trial consisted of testing 3 martens, and then swapping structural cues for the last 2 martens. If cage effects were present, the strength of selection for structural cues should be different for the 2 structural arrangements. Marten foraging responses were tested under 3 different arrangements of structural cues during the summer of 1993. Trial 1 tested for the influence of both structural and overhead cues on perceived risk. For the first trial half the arena had both vertical structure (stems) and overhead cover (tarp), the other half had no structural cues. Trial 2 was a test to contrast the effect of stem and overhead cues. For the second trial half the trial arena had only stem structure and the other half had only overhead cover. The third trial also contrasted the

effect of stem and overhead cues, but included the addition of a predator cue to increase perceived risk and emphasize differences between cues. Trial 3 had the same arrangement of vertical structure (stems) and overhead cover (tarp) as trial 2, with the addition of a predator cue (coyote scats were simultaneously placed in each half of the trial arena). All trials lasted for 10 minutes, with the clock starting from the point at which martens actually entered the arena. After the trial was completed, I made visual contact with test subjects by looking over the pen wall directly opposite the entrance used by martens. This prompted martens to return through the access tube to their pens.

Statistical analysis of trials

I tested for a cage effect by comparing consumption of bait with an initial arrangement of structural cues, and then with structural cues reversed. A t-test was used to compare bait consumption at feeding trays for all trials by arena half. If 1 of the arena halves was more attractive to martens there should be significantly greater consumption of bait in that half. Thus, biases due to differences in arena halves could be detected and, if necessary, factored out. I used randomization tests (Noreen 1989) to evaluate whether differences in cover types affected the consumption of baits by martens during summer. Captive trials also allowed me to test the responses of martens to a specific predatory cue. Statistical distributions for all comparisons between marten consumption of bait by cover type were created using the equation (1). For within-trial comparisons, S is the test statistic based on the absolute value of differences between mean bait consumption for each structural cue, x is a random sample of bait consumed from cover-type _{x} and y is a random sample of bait consumed from cover-type _{y} for all martens in a

given trial. The numbers of samples from each cover type were n_x and n_y . The number of randomly sampled test statistics greater than or equal to the actual statistic divided by the number of random samples provides an approximate probability. To evaluate the effect of a predatory cue, trials 2 and 3 were compared using an equation similar to that used to test for differences within trials. In this test, \underline{S} is the test statistic based on the absolute value of differences between mean bait consumption by trial, x and y are random samples from actual consumption of bait from the 2 trials, and n_x and n_y are the numbers of samples from each trial. Probability distributions for tests of captive trials were derived from 2000 random simulations. An alpha level of 0.05 was used to assess significance for all tests.

RESULTS

Field Experiments

Micro-habitat data collected around bait-boxes indicated that overhead cover differed between all habitat classes; highest overhead cover measurements were recorded in coniferous forest, lowest were made in open habitats with defoliated habitats falling between these 2 extremes due to Defoliated and burned stands still possessed low levels of overhead cover from remaining horizontal branches (Fig. 1). Within habitat classes, there were no differences between study sites. The number of stems were similar for coniferous and defoliated habitats and lower for open habitats (Fig. 2). These measurements suggested that my classification

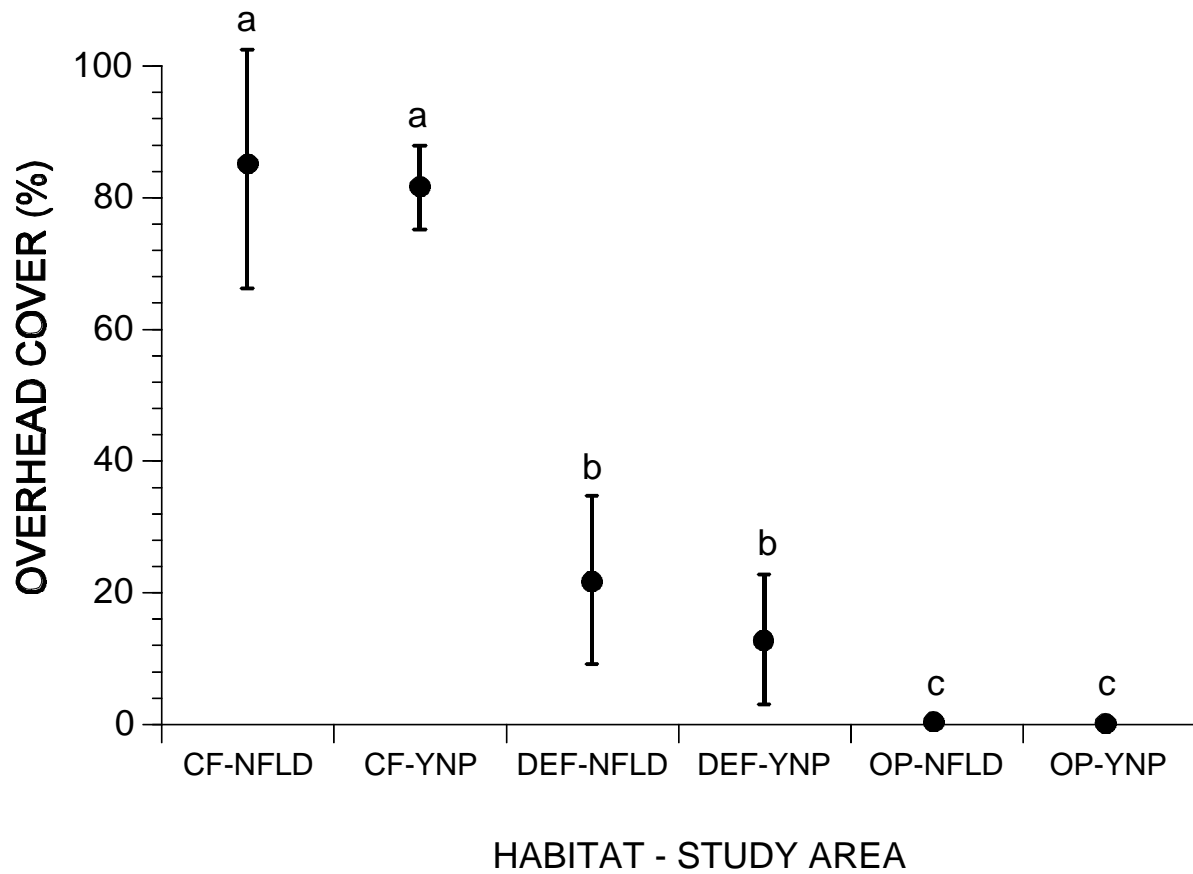


Figure 1. Overhead cover measured at bait-box locations (means \pm 1 SE). Bars sharing the same letters are not statistically different (Tukey, $P > 0.05$). CF-NFLD = coniferous forest - Newfoundland (n=9), DEF-NFLD = defoliated - Newfoundland (n=6), OP-NFLD = open - Newfoundland (n=9), CF-YNP = coniferous forest - Yellowstone National Park (n=9), DEF-YNP = defoliated - Yellowstone National Park (n=9), OP-YNP = open - Yellowstone National Park (n=9).

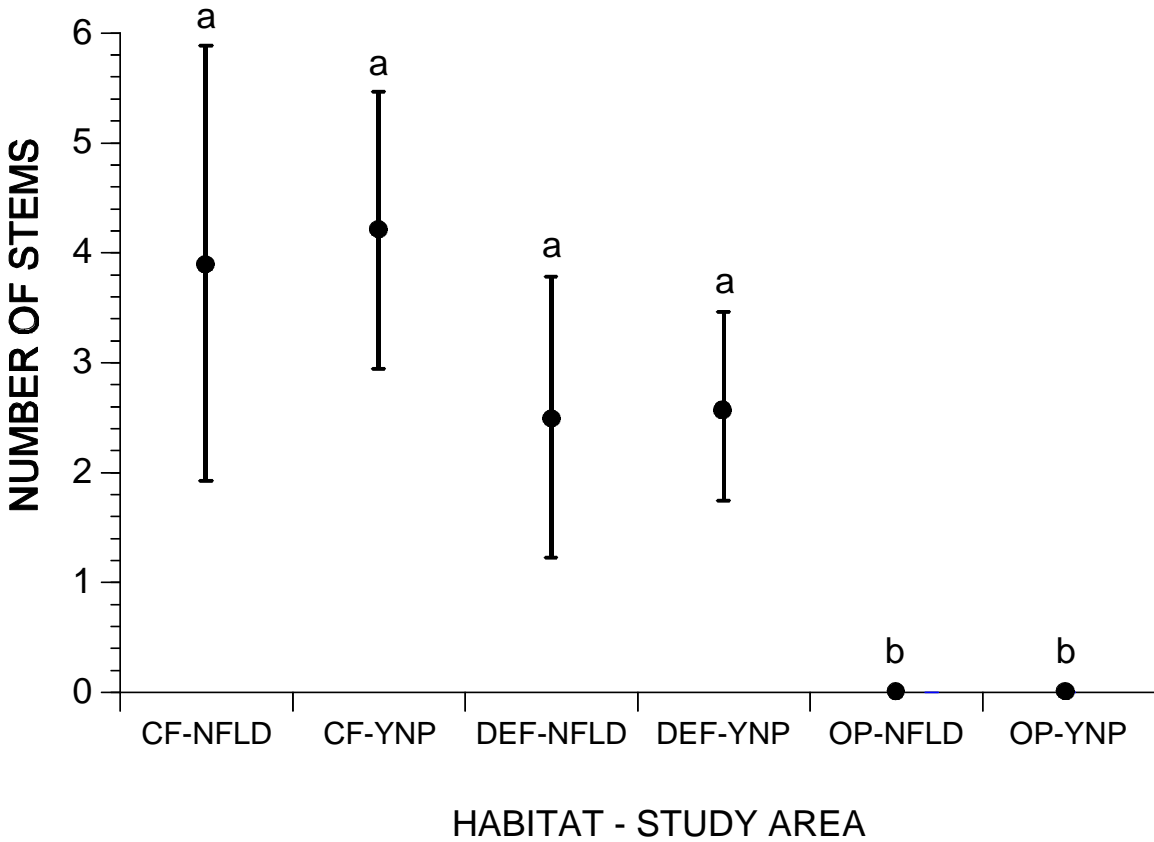


Figure. 2. Number of stems >10 cm dbh found within a 5 m radius of bait-boxes (means \pm 1 SE).

Bars sharing the same letters are not statistically different (Tukey, $P > 0.05$). CF-NFLD = coniferous - Newfoundland (n=9), DEF-NFLD = defoliated - Newfoundland (n=6), OP-NFLD = open - Newfoundland (n=9), CF-YNP = coniferous - Yellowstone National Park (n=9), DEF-YNP = defoliated - Yellowstone National Park (n=9), OP-YNP = open - Yellowstone National Park (n=9).

scheme was effective in separating habitats by their overhead cover and stem structure characteristics. Thus habitat comparisons could decouple the individual influences of these factors.

Habitat use

Marten use of bait-boxes by habitat showed significant differences ($P = 0.001$, $n = 3$, $NS = 1000$). By controlling availability of food and the minimal potential for increased thermal costs. The result is compelling evidence for variable perception of risk by marten based on habitat characteristics. Based on this result, I rejected H_01 "habitat associations of marten are not based on perceived risk of predation" and proceeded to test H_02 .

Foliar cover

The comparison of coniferous and defoliated forest failed to detect any difference in visitation at any distance. This failure to reject H_02 suggests that martens in my study areas failed to recognize a lack of foliar cover as influencing their exposure to predation risk (Fig. 3). Based on this result I proceeded to look at H_03 and the influence of stem structure on marten habitat use.

Stem structure

Marten visitation rates differed significantly between defoliated forest and open areas as distance into habitats increased (Fig. 4). This suggests that marten perceive the presence of large stems as a moderating influence on predation risk. However, this test could not identify how stems limited risk to marten, i.e., concealment, escape cover, or both.

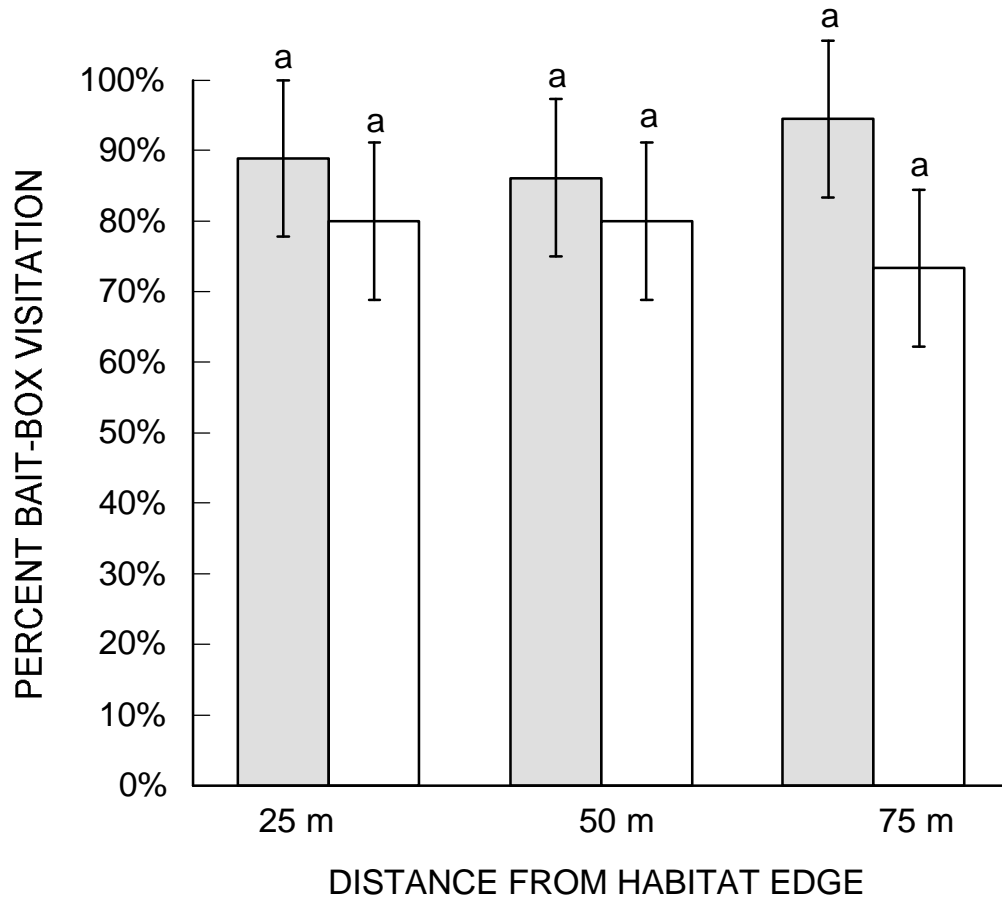


Fig. 3. Comparison of marten use of bait-boxes in coniferous forest and defoliated coniferous forest to evaluate the influence of foliar cover on martens habitat use (means \pm 1 SE). Bars sharing the same letters are not statistically different (Tukey, $P > 0.05$). \blacksquare : coniferous forest ($n = 6$); \square : defoliated coniferous forest ($n = 5$).

Figure 3

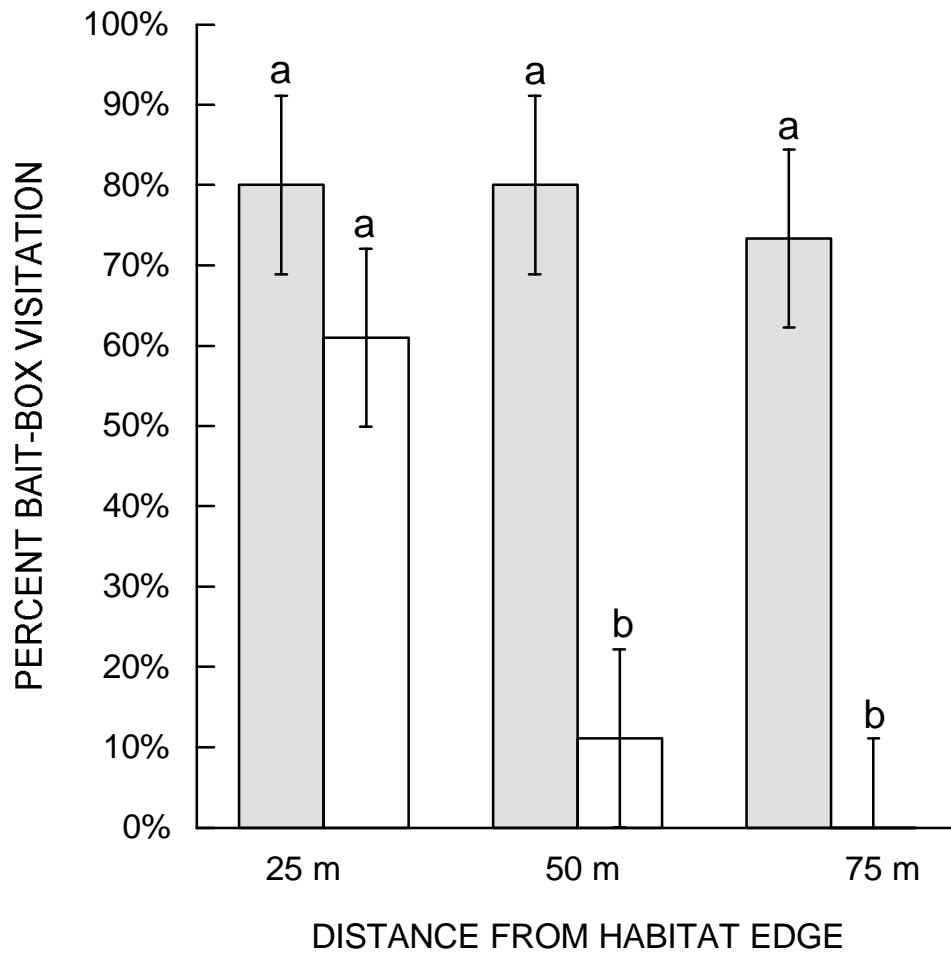


Fig. 4. Comparison of marten use of bait-boxes in defoliated coniferous forest and open habitats to evaluate the influence of stem structure on marten habitat use (means ± 1 SE). Bars sharing the same letters are not statistically different (Tukey, $P > 0.05$). \blacksquare : coniferous forest ($n = 6$); \square : defoliated coniferous forest ($n = 6$).

Field observations

In addition to experimental tests I collected detailed observations on the approach of marten to and from bait boxes. These data provided strong confirmation that marten perceived open habitats as more dangerous than either coniferous or defoliated forest. When faced with bait-boxes in open habitats, marten always approached from the forest and traveled in a straight line to and from boxes (n=17). I also noted that marten would follow the edge of the forest to both sides of the direct line of approach, apparently in an attempt to find a way to get closer to the more distant boxes. When bait-boxes were placed in coniferous habitats, marten were more likely to approach and/or leave transects from the forest interior. Defoliated stands did not appear to elicit any preference for marten approach or exit. This apparent lack of orientation in the movements of marten to and from transects in defoliated stands suggests that they do not perceive defoliated habitats as inherently risky. In addition, 1 collared marten was killed at the Newfoundland study site by a red fox (Vulpes vulpes). A previous study in the same area (1986-1988) documented 2 marten mortalities, 1 attributed to red fox and 1 unknown, as well as 1 failed predatory attack (Bissonette et al. 1988).

Captive Experiments

Trial arena effects

Marten consumption of bait was similar on both sides of the arena ($t = 0.128$, $P = 0.899$, $d.f. = 28$), indicating that the arena did not introduce a measurable bias to the trials. Based on this result I did not block the data by arena halves.

Trial 1: overhead cover & stem structure vs. no structure

When presented with a choice of foraging in the half of the arena with both overhead cover and woody stem structure or the half with no structure, martens showed a strong preference for the combination of cover structures ($P = 0.013$, $n = 5$, $NS = 2000$, Fig. 5). Results were conclusive, with all animals consuming more bait from the arena half with cover. Arena halves lacking both overhead cover and stem structure apparently failed to provide martens with the cues associated with usable habitat. This suggests that tested martens perceived areas lacking structural cues common to coniferous forests (overhead cover and coarse woody stem structure) as more dangerous.

Trial 2: foliar cover vs. stem structure

Having established that martens did perceive differential risks between a combination of overhead and structural cover vs. no cover, I attempted to separate the effects of overhead cover and stem structure in trial 2. However, the results of the second trial were ambiguous. While individual martens appeared to prefer either overhead cover or stem structure, as a group, they did not exhibit a preference ($P = 0.671$, $n = 5$, $NS = 2000$, Fig. 5).

Trial 3: foliar cover vs. stem structure with predator cues

The addition of 2 coyote scats, 1 to each half of the trial arena, produced an unexpected result. I had hypothesized that encountering some cue indicating the proximity of a predator would prompt marten to show greater preference for either overhead cover or large woody stem structure based on which provided them the greatest protection from predators. However, coyote scats did not appear to influence marten choice between cover types ($P = 0.999$, $n = 5$, $NS = 2000$). Instead of influencing their choice of cover type, the addition of

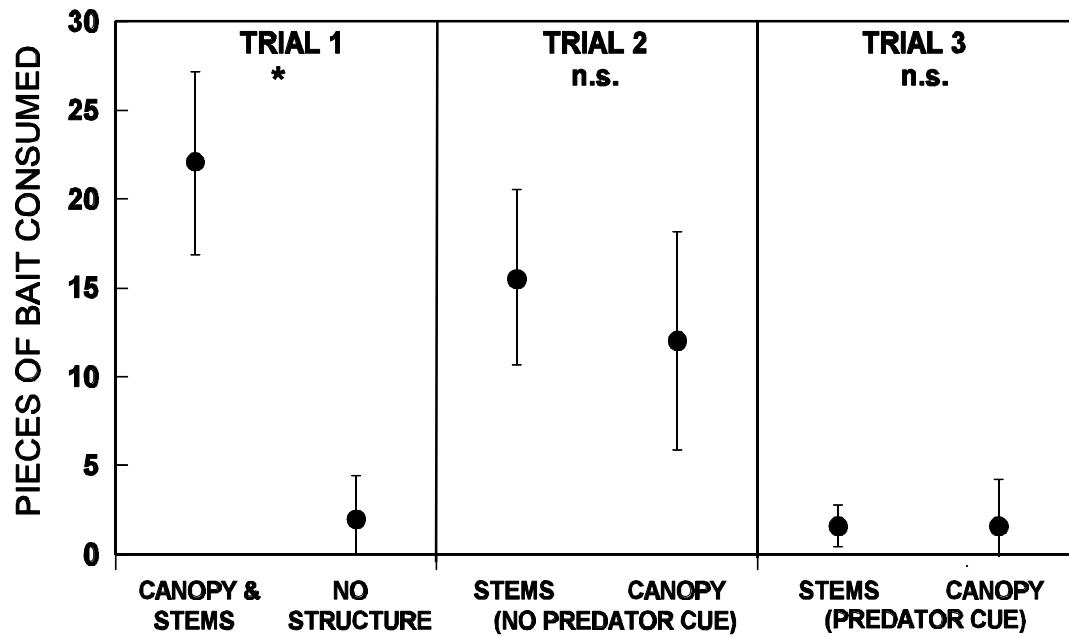


Figure. 5. Mean bait consumption by 5 martens (3:♂, 2:♀)(±1 SE) in 3 trials: trial 1; overhead cover and stem structure vs. no structural cues, trial 2; stem structure vs. overhead cover, and trial 3; which was identical to trial 2, but included a predator cue.

* = $\underline{P} < 0.05$, n.s. = not significant

the predator cue (coyote scats) appeared to cause a general decreased in marten bait consumption (Fig. 5). Martens limited their movement from the access tube entrance and displayed increased vigilance.

Trial 2 vs. trial 3: predator cues vs. no predator cues

As suggested by the plots of trials 2 and 3 (Fig. 5), there was a significant difference between the amounts of bait consumed in trial 2 and trial 3 ($P = 0.004$, $n = 10$, $NS = 2000$). Martens had a strong negative reaction to the additional cue (coyote scats) suggesting perception of additional risk. In addition, during trial 3, martens demonstrated behaviors suggesting increased vigilance. They spent little or no time foraging and generally remained close to the pen entrance. When martens did forage, they tended to grab a single piece of bait in their mouths and run back to the pen entrance before consuming it. These behaviors were in marked contrast to martens foraging in the previous 2 trials, where bait usually was consumed while martens stood in the feeding trays.

DISCUSSION

Population Differences

Martens in this study came from 3 distinct populations, separated by as much as 5,800 km. In addition, the island of Newfoundland has been separated from the North American mainland since the last ice age, suggesting that the marten on the island have been genetically isolated. I had expected some variation in marten response by study area, however, patterns of bait-box visitation by martens in Newfoundland and YNP, as well as the results of captive trials in Utah, suggested that these different populations share similar habitat requirements. Although the specific tree species and their size varied for the coniferous forests inhabited by the 3 populations tested, they

all contained numerous large stems, abundant coarse-woody-debris and abundant overhead cover.

Winter Habitat Cues

Although overhead cover has been considered important to the habitat selection of marten (Koehler and Hornocker 1977, Allen 1984), I found no evidence that martens perceived defoliated coniferous forest as different from intact coniferous forest with regard to predation risk. Given their small mass (500 - 1,400 gm), I anticipated that martens would be sensitive to the risk of avian predation. However, most of the avian predators in Newfoundland and Yellowstone study areas migrate south during the winter. Marten may be more sensitive to the risk of avian predation during the summer when raptors are more common.

While American marten have long been recognized as an obligate coniferous forest species, previous studies were purely observational and unable to determine the cause(s) for this behavior. By controlling food availability through baiting, I was able to isolate the influence of perceived risk through the manipulation of habitat cues. Surprisingly, martens did not perceive a lack of overhead cover as an increased risk during the winter. Conversely, the lack of large stems and complex physical structures all but excluded them. Only 1 marten ever visited a bait-box 50 m from the forest edge into a clearing, and none ever visited boxes 75 m from the forest edge. The cause for this close association between marten and large complex stem structure may be twofold. First, marten will climb trees when threatened. In conifer forests, with their tight branching structure, this strategy would work against both terrestrial and avian predators. Secondly, forest habitats characterized by large complex stem structure may provide some measure of concealment

from potential predators. Martens select habitats perceived as less risky, even when this avoidance had energetic costs. The stereotypical response to specific habitat characteristics suggests that the preference of marten for coniferous forests is linked to an anti-predation strategy.

Summer Habitat Cues

The results of the first captive experiment (stems and overhead cover vs. no stems or overhead cover) indicate that martens perceived refuge qualities in the portion of the trial arena emulating coniferous forest (stems and cover). This supports the hypothesis that martens identify coniferous forests as less risky in summer as well as winter. Furthermore, captive tests indicated that the scale at which martens made their assessments of predation risk was extremely fine. The straight-line distance between feeding trays in the trial arena was only 6 m. This fine-scale, imposed on trials by the limited size of the trial arena, may have limited my ability to tease apart the separate influences of overhead cover and stem structure.

Although previous trials suggested that observed marten behaviors were linked to a “lifestyle” that limited their exposure to predation risk, the final trial provided an opportunity to test for the response of martens to a more direct predator cue. When confronted with the predator cue, every marten tested showed a strong and immediate decrease in activity and an increase in vigilance.

The life history of marten provides clues to the potential influences of predation. Marten typically do not breed until their second or third year of life and can live to 14 years. While marten must balance requirements for foraging and thermal homeostasis with risk of predation, the asymmetric costs of predation strongly bias a K-selected species toward overestimation of

predation risk (Bouskila and Blumstein 1992).

Conclusions

These experiments demonstrated that American martens do perceive the structural habitat cues of coniferous forest as conveying some decreased risk of predation and that perception is not seasonally limited. Martens were unwilling or unable to make extensive use of food resources in habitats lacking structure in both summer and winter. Surprisingly, overhead cover did not appear to influence martens use of habitats in either Newfoundland or YNP, though this may be related to the absence of avian predators during the winter in these areas. Captive trials were unable to resolve differences between martens response to overhead cover and stem structure cues, though the source of security cover in coniferous forests during the winter appears to be primarily large woody stems and debris. The uniform reaction of all martens tested for their response to a direct predator cue also were highly sensitive to direct predator cues and they responded by limiting activity and increasing vigilance. The recognition of the martens dependency on specific habitat characteristics should be investigated further with an emphasis on detecting threshold values for stem structure and larger scale testing of the value of overhead cover during the summer.

LITERATURE CITED

Allen, A. W. 1984. Habitat suitability index models: marten. U.S. Fish and Wildl. Serv.

FWS/OBS-82/10.11. Washington D.C. Revised. 13 pp.

Bissonette J. A., Fredrickson, R. J. & Tucker, B. J. 1988. The effects of forest harvesting on marten and small mammals in western Newfoundland. Report prepared for the Newfoundland

and Labrador Wildlife Division, and Corner Brook Pulp and Paper Company, Limited. Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, UT. 109 pp.

- Bouskila, A. & Blumstein D. T. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am. Nat.* **139**:161-176.
- Brown, J. S., Kotler, B. P. Smith, R. J. & Wirtz, W. O. II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia.* **76**:408-415.
- Buskirk, S. W., 1984. Seasonal use of resting sites by marten in South-Central Alaska. *J. Wildl. Manage.* **48**:950-953.
- Buskirk, S. W., & McDonald, L. L. 1989. Analysis of variability in home range size of the American marten. *J. Wildl. Manage.* **53**:997-1004.
- Buskirk, S. W., Forrest, S. C., Raphael, M. G. & Harlow, H. J. 1989. Winter resting ecology of marten in the central Rocky Mountains. *J. Wildl. Manage.* **53**:191-196.
- Cambell, T. M. 1979. Short-term effects of timber harvests on pine marten ecology. M.S. Thesis, Colorado State Univ., Fort Collins. 71pp.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology* **61**:119-128.
- Davis, M. H. 1983. Post-release movements of introduced marten. *J. Wildl. Manage.* **43**:850-860.

de Vos, A. 1952. Preliminary live-trapping studies of marten. *J. Wildl. Manage.* **16**:207-215

Douglass, R. J., Fisher, L. G. & Mair, M. 1983. Habitat selection and food habits of marten *Martes americana*, in the Northwest Territories. *Can. Field Nat.* **97**:71-74.

Edwards, J. 1983. Diet shifts in the moose due to predator avoidance. *Oecologia.* **60**:185-189.

Francis, G. R. & Stephenson, A. B. 1972. Marten ranges and food habits in Algonquin Provincial Park, Ontario. *Minis. of Nat. Resour. Res. Rep.* 91, 53 pp.

Hawley, V. D. & Newby, F. E. 1957. Marten home ranges and population fluctuations. *J. Mammal.* **38**:174-184.

Hargis, C. D. & McCullough, D. R. 1984. Winter diet and habitat selection of marten in Yosemite National Park. *J. Wildl. Manage.* **48**:140-146.

Herman, T. & Fuller, K. 1974. Observations of the marten (*Martes americana*), in the Mackenzie District, Northwest Territories. *Can. Field-Nat.* **88**:501-503.

Koehler, G. M. & Hornocker, M. G. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *J. Wildl. Manage.* **41**:500-505.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* **68**:689-701.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under risk of predation: a review and

prospectus. *Can. J. Zool.* **68**:619-640.

Mech, L. D. & Rodgers, L. L. 1977. Status, distribution and movements of martens in northeastern Minnesota. USDA For. Serv. Res. Paper NC-143, North Cent. For. Exp. Sta., St. Paul, Minn. 7 pp.

Murie, A. 1961. Some food habits of the marten. *J. Mammal.* **42**:516-521.

Noreen, E. W. 1989. Computer intensive methods for testing hypotheses: an introduction. J. Wiley & Sons, New York. 229pp.

Nyholm, E. S. 1970. On the ecology of pine marten (*Martes martes*) in eastern and northern Finland. *Suomen Riista* **22**:105-118. (In Finnish, with English summary).

Pulliainen, E. 1981. Winter habitat selection, home range, and movements of the pine marten, *Martes martes* in a Finnish Lapland forest. Pages 1068-1087 in Proceedings of the Worldwide Furbearer Conference, Frostburg, MD. J. A. Chapman & D. Pursley eds.. R. R. Donnelley and Sons Company, Falls Church, Virginia.

Raine, R. M. 1982. Ranges of juvenile fisher, *Martes pennanti*, and marten, *Martes americana*, in southeastern Manitoba. *Can. Field-Nat.* **96**:431-438.

Rowe, J. S. 1959. Forested regions of Canada. Dept. Northern Affairs and Nat. Res., Forestry Br. Bull. 123. 71 pp.

Seal, U. S., Thorne, E. T., Bogan, M. A. & Anderson, S. H. 1989. Conservation biology and the

- black-footed ferret. Yale Univ. Press. New Haven, CT. 302 pp.
- Sherburne, S. S. 1992. Marten use of Subnivean access points in Yellowstone National Park, Wyoming. M.S. thesis, Utah State University, Logan. 37 pp.
- Sherburne, S. S., & Bissonette, J. A. 1994. Marten subnivean access point use: response to subnivean prey levels. *J. Wildl. Manage.* **58**:400-405.
- Sih, A. 1980. Predators and prey lifestyles: An evolutionary overview. Pages 203-224 in *Predation: direct and indirect impacts on aquatic communities*. W.C. Kerfoot & A. Sih, eds. Univ. Press of New England, Hanover, N.H.
- Snyder, J. E. & Bissonette, J. A. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. *Can. J. Zool.* **65**:169-174.
- Soutiere, E. C. 1979. Effects of timber harvesting on martin in Maine. *J. Wildl. Manage.* **43**:850-860.
- Spencer, W. D., Barrett, R. H. & Zielinski, W. J. 1983. Marten habitat preferences in the northern Sierra Nevada. *J. Wildl. Manage.* **47**:1181-1186.
- Steventon, J. D. & Major, J. T. 1982. Marten use of habitat in a commercially clear-cut forest. *J. Wildl. Manage.* **46**:175-182.
- Thompson, I. D. 1991. Could marten become the spotted owl of eastern Canada? *Forest. Chron.* **67**:136-140.

- Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. *J. Wildl. Manage.* **58**:280-288.
- Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**:1540-1548.
- Wiens, J. A., Rotenberry, J. T., & Van Horne, B. 1986. A lesson in the limitations of field experiments: substeppe birds and habitat alteration. *Ecology* **67**:365-376.
- Zielinski, W. J., Spencer, W. D. & Barrett, R. H. 1983. Relationship between food habits and activity patterns of pine martens. *J. Mammal.* **64**:387-396.

CHAPTER V

Summary

Although the preference of American martens for coniferous forests is widely recognized, the mechanisms responsible for this relationship have remained largely untested. My research program systematically addressed the causes for and implications of this association. I began by testing the habitat selection of American martens in Newfoundland, and confirmed that they preferred coniferous forests that contained large trees and abundant coarse woody debris (CWD). More importantly, I was able to determine that the scale at which this selection occurs is quite small. Composition of habitats was significantly different at distances greater than 80 m from used habitats. The actual scale of selection may be even smaller, but my ability to detect it was limited by the resolution of the remote sensing device used, the classification scheme, and the natural variability of study areas habitats. This result suggests that both foraging and non-foraging movements of martens are linked intimately to surrounding forest structure. Factors operating at some larger scale, e.g., thermally advantageous resting sites, are not sufficient to explain this resolution of selection.

The use of thermally efficient subnivean resting sites appears to be a behavioral strategy used by martens to limit their thermal costs. However, resting sites offer only limited thermal protection; ground level temperature under snow cover are approximately 0°C. If thermoregulatory factors were dictating the actions of martens, they should adjust their activity patterns to limit energetic costs. However, martens in Newfoundland failed to minimize these costs. Marten food habits failed to provide any evidence that martens were synchronizing their activity patterns with that of their prey. Alternatively, I found that martens suffer a real threat of

predation as evidenced by the 2 known cases of predation by red fox. Although activity patterns of red fox were not measured, they were seen commonly during the daylight hours. Martens may experience some decreased risk by being less detectable at night. Additionally, martens are relatively long-lived and late in reaching sexual maturity, suggesting that the risk of mortality could be stronger proximate influence than energetic constraints.

Based on these findings, a field experiment was used to test whether martens were constrained to coniferous forests by access to food resources or predation risk. Martens in Newfoundland and Yellowstone National Park showed similar responses, consistent with the hypothesis that they perceived decreased predation risk in coniferous forest habitats. Martens did not perceive a lack of foliar cover as a limiting factor in accessing baits, but did limit their use of baits in habitats devoid of complex woody-stem-structure. The source of security cover in old/mature forests appears to be large woody stems and possibly coarse woody debris..

The field experiments in chapter 4 provided strong evidence that during winter, martens perceive some increased risk outside of late-seral coniferous forest habitats, but they could not provide any indication of the influence of predation risk during the snow-free period. While I was unable to determine which structural feature was most important to martens during the summer, captive experiments demonstrated that martens perceive late-seral coniferous forest habitats as less dangerous. Together, field and pen experiments (chapter 4) provide compelling evidence that martens are cognizant of predation threats year-round. I was also able to detect a strong restriction in foraging activity in response to a predator cue.

American martens make their habitat selection decisions on a fine scale. Although they must take both thermal conditions and prey availability into account, my research suggests that these

factors were not the primary influences for observed marten behaviors. Instead, martens from 3 distinct areas demonstrated a consistent sensitivity to predation risk. Martens selection of habitats, in part, reflect the indirect effect of predation risk. Structures that provide them with either concealment or escape cover are selected. Additionally, martens can and will modify other behaviors to limit detection as perceived risk increases.