

Home-range size and habitat selection by American marten (*Martes americana*) in Labrador

Adam C. Smith and James A. Schaefer

Abstract: Variation in home-range size can be related to different factors at different spatial scales. This study examined the patterns of home-range size and habitat selection of American marten (*Martes americana*) in southeastern Labrador, a region of extensive and pristine forests. Over 1.5 years, we monitored 28 radio-collared marten and compared the availability of habitat types with their use. Marten avoided areas with low productivity and low canopy cover (<20%) but showed no selection for tree species composition or cover among more productive forests. Mean home ranges for both sexes (males, 45.0 km²; females, 27.6 km²) were exceptionally large, more than double the largest values previously recorded for the species. We analyzed variation in home-range size at two scales: within our study population and, using data from the literature, among populations across the species range in relation to temperature, snow cover, and body size. Within our population, home-range area was positively related to the proportion of bog and less productive, scrub forests in the home range. Among populations, differences in home-range size were not significantly related to any of the tested factors.

Résumé : La variation de taille du domaine peut être reliée à différents facteurs, à des échelles spatiales différentes. Nous avons examiné la taille des domaines et le choix d'habitat chez des martes d'Amérique (*Martes americana*) dans le sud-est du Labrador, une région de forêts étendues et encore intactes. Pendant une période de 1,5 années, nous avons suivi 28 martes porteuses d'un émetteur radio et étudié l'utilisation des habitats en fonction de leur disponibilité. Les martes évitent les zones de faible productivité et à couverture végétale trop clairsemée (<20 %), mais ne montrent de préférence ni pour une composition particulière d'espèces d'arbres, ni pour un type défini de couverture végétale dans les forêts plus productives. La taille moyenne des domaines a été évaluée à 45,0 km² pour les mâles et à 27,6 km² pour les femelles, mesures équivalentes au double des valeurs enregistrées auparavant chez cette espèce. Nous avons analysé les variations de taille des domaines à deux échelles, chez la population étudiée et, d'après les données de la littérature, chez les populations de toute l'aire de répartition de l'espèce, en fonction de la température, de l'épaisseur de la couche de neige et de la taille du corps. Chez la population du Labrador, la surface des domaines est en corrélation positive avec la proportion de la surface occupée par les tourbières ou par les boisés buissonneux et moins productifs. Chez les autres populations, les différences de taille entre les domaines ne sont reliées significativement à aucun des facteurs étudiés.

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Introduction

The size of an animal's home range may be affected by many factors, including climate (Lindstedt et al. 1986), food (Taitt 1981; Sturtevant and Bissonette 1997), population density (Wolff 1993), body size (Harestad and Bunnell 1979), and social organization (Damuth 1981). To add to this complexity, these factors may operate within a hierarchy of scales (McLoughlin and Ferguson 2000). Variation in home-range size within populations is nested within the variation among populations, which in turn, is nested within the variation among species. Home-range size may be a reflection of limiting factors acting at these three scales. Among

species, home-range size is governed primarily by body size (Calder 1984; McLoughlin and Ferguson 2000). Among populations, productivity of the environment can exert a strong influence (Lindstedt et al. 1986; McLoughlin and Ferguson 2000), whereas within a population, habitat productivity and food availability seem to be the primary factors. However, sex, social factors, and density can have strong effects (Taitt 1981; Powell et al. 1997; McLoughlin and Ferguson 2000).

The American marten (*Martes americana*) presents a useful test case of some of these ideas. The species inhabits many of the forested regions of Canada and south into the mountainous regions of the western United States (Strickland and Douglas 1987). Across the species' range, there is wide variety in forest types that are occupied, reflected by variability in patterns of habitat selection (Buskirk and Powell 1994; Bissonette et al. 1997; Potvin et al. 2000). Although there is often a strong association between marten and dense-canopy coniferous forests (Strickland and Douglas 1987; Buskirk and Powell 1994), some researchers have suggested that marten do not require, or even prefer, dense coniferous cover. Rather, vertical and horizontal structure (granting access to small mammal prey and the avoidance of

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A.C. Smith. Watershed Ecosystem Graduate Program, Trent University, Peterborough, ON K9J 7B8, Canada.

J. A. Schaefer.¹ Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.

¹Corresponding author (e-mail: jschaefer@trentu.ca).

predators) may be more important (Chapin et al. 1997; Potvin et al. 2000).

Within and among populations, marten exhibit large variations in home-range size, sometimes in concert with differences in environmental conditions and body size. For example, there may be a negative relationship between home-range size and prey abundance within a population (Thompson and Colgan 1987), and territories with higher proportions of avoided or suboptimal habitat types tend to be larger (Soutiere 1979; Thompson and Colgan 1987). Among populations, variation in home-range size may be related to habitat quality, productivity, or body size (Buskirk and McDonald 1989).

To test potential factors affecting marten home-range size, as well as to further examine habitat selection, we chose to study the species close to its geographical and environmental limits, in southeastern Labrador (Fig. 1). Here, the taiga has remained essentially undisturbed by human activities, yet it is also comparatively unproductive and has low levels of canopy cover and structural complexity (Foster 1984). Stands with relatively dense cover and complex structure are small and isolated within a matrix of unproductive, structurally simple, open-canopy forest (Foster 1983) that marten in other parts of their range tend to avoid (Buskirk and Powell 1994). We therefore hypothesized that marten in Labrador would show habitat preferences for areas of high canopy cover and avoidance of areas of low canopy cover. The low productivity also led us to hypothesize that marten in Labrador would have larger home ranges compared with populations elsewhere. To test alternative hypotheses for explaining intraspecific variation in home-range size, we updated the analysis of Buskirk and McDonald (1989) with more recently published data. We looked for relationships, among North American populations, between home-range size and snow cover, temperature, and body size at this large scale.

Material and methods

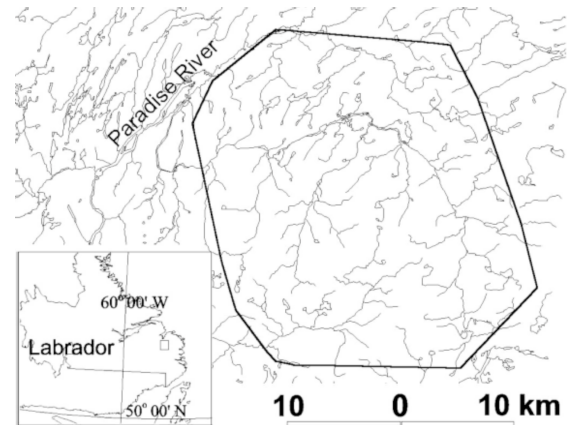
Study area

The 750-km² study area was situated in southeastern Labrador (53°20'N, 57°20'W; Fig. 1). The mean temperature (1961–1990) for January was –13.8°C, and for July, 12.3°C. Snow cover lasted from mid-October until early May, with an average annual snowfall of 440 cm (Environment Canada; 30-year climatic norms).

The study area was composed primarily of open-canopy black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) forests, with a few much smaller stands of white birch (*Betula papyrifera*). Almost all forested areas were >80 years old with the exception of a small burned area in the northwest corner of the study area, which burned in 1956 (Foster 1983).

The area included two established trap lines that were active during the second winter of the study. Construction of the Trans-Labrador Highway began along the northern border of the study site during the summer of 1999. The road construction had no direct impact on access to the study area during the study. The study area was not directly exposed to any other human activity. It was accessible on snowmobile during the winter but was essentially inaccessible by land between April and December.

Fig. 1. Map of the study area in southeastern Labrador, Canada.



Capture and radio-tracking

Marten were captured in Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wis., U.S.A.). Tomahawk 206 (75 × 25 × 25 cm) and Tomahawk 204 (45 × 18 × 18 cm) traps were placed opportunistically along trails scattered throughout the study area. The traps were baited with canned sardines and checked daily. Trapping periods were in October 1998, January–March 1999, and August–September 1999.

Captured animals were run into a handling cone (Bull et al. 1996) and immobilized with 0.12–0.19 mL of 100 mg/mL ketamine hydrochloride solution. Marten were then weighed, sexed, and injected with a subcutaneous microchip for individual identification (PIT tag; AVID Canada, Calgary, Alta., Canada), and the first premolar was removed for cementum ageing (Matson's Laboratory, Milltown, Mont., U.S.A.). Marten were fitted with a 35 g VHF radio collar (Lotek Engineering, Newmarket, Ont., Canada). Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993). A two-way, fixed-effects analysis of variance (ANOVA) was performed to test for significant effects of age and sex on the mass of captured marten (Sokal and Rohlf 1995).

Relocation of radio-collared marten was attempted every 2 weeks from a fixed-wing aircraft from December 1998 – March 2000 (median interval = 11 days). Locations were generated using the plane's onboard Global Positioning System (GPS). The accuracy of aerial locations was estimated by placing collars, in standard signal mode, in different habitat types at locations unknown to observers. Locations for test collars were generated using the same techniques as those used for locating collared animals and were compared with locations determined on the ground with a differentially corrected GPS.

The abundance of small mammals in the study area was determined in September 1998 and 1999. Three transects were established, each composed of 11 trap stations, 10 m apart. At each station, a Museum Special trap was baited with peanut butter and oats and set for 3 consecutive nights. Species were identified by dental and pelage characteristics.

Home range and habitat selection

Marten annual home-range estimates were described by 100% minimum convex polygons to facilitate comparison

Table 1. Vegetation characteristics of habitat types in the study area in southeastern Labrador.

Stand type	Dominant species composition	Canopy cover (%)	Age (years)
Burn	Black spruce – balsam fir	<40	<50
Bog	Black spruce – balsam fir	0–10	NA
Scrub	Black spruce – balsam fir	<20	>50
Medium mixed	White birch >25%	20–40	<120
High mixed	Black spruce – balsam fir <75%	41–70	<120
	White birch >25%		
Medium spruce–fir	Black spruce >25%	20–40	>150
	Balsam fir >25%		
High spruce–fir	Black spruce >25%	41–70	>150
	Balsam fir >25%		
Medium spruce	Black spruce >75%	20–40	>150
High spruce	Black spruce >75%	41–70	>150

Note: NA, not available.

with previous studies (Raine 1982; Buskirk and McDonald 1989; Latour et al. 1994; Potvin and Breton 1997) and to accommodate the relatively small number of locations per animal resulting from the isolation of our study site.

The habitat composition of the study area was determined using forest stand inventory maps created by the Newfoundland and Labrador Department of Forest Resources and Agrifoods. Forest characteristics included the species composition and canopy cover. Forests types were grouped into one of nine classes (Table 1). All spatial analyses were conducted using ARC View GIS 3.1 (ESRI, Redlands, Calif., U.S.A.).

The use of each habitat class relative to abundance was analyzed using a chi-square technique and Bonferroni confidence intervals (Neu et al. 1974). Data for all 28 marten were pooled because of the small number of locations per individual ($n = 16.5 \pm 4.6$ SD; White and Garrott 1990). Available habitat was defined as that within all individual home ranges.

Means are reported with their associated standard deviations (mean \pm SD). All statistical tests were two-tailed unless otherwise noted.

Variation in home-range size

Linear regression was used to compare home-range size with body size and with the proportion of avoided habitat types in each home range. We also analyzed the effects of sex and age on home-range size using a two-way fixed-effects ANOVA.

To analyze the variation in home-range size among populations, published data on mean home-range sizes for other marten populations were compared with environmental and body-size data using linear regressions (Sokal and Rohlf 1995). Data on climate were 30-year norms for the monitoring station nearest the study site from Environment Canada or the National Climate Data Center in the United States. Because marten are thought to be limited in their activities by thermal requirements (Bateman 1986; Buskirk et al. 1988; Buskirk and Taylor 1994), we chose to examine the effects of temperature by using January mean temperatures as an index of severity. Another important factor for marten is their ability to access small mammal prey under the snow

Table 2. Mass (mean \pm SD) of male and female adult (>1 year old) and juvenile radio-collared American marten (*Martes americana*) in southeastern Labrador.

	Male		Female	
	<i>n</i>	Mass (g)	<i>n</i>	Mass (g)
Adult	5	1305 \pm 119.1	6	850 \pm 115.1
Juvenile	8	1181 \pm 85.3	8	798 \pm 99.8

(Raine 1987; Wilbert et al. 2000). To examine the effects of snow cover, we used two measurements, the number of months of continuous snow cover and mean annual snow-fall. The duration of snow cover should be an indicator of the length of the season during which access to subnivean prey is limited.

Results

We captured 28 marten: 5 adult (>1 year old) males, 6 adult females, 8 juvenile females, 8 juvenile males, and 1 female that was not aged because of difficulties obtaining a tooth for cementum analysis. Of the juveniles, 15 were collared in the late winter (March 1999) and were considered adults for most of the study. The remaining juvenile was collared the following summer but survived only 4 months after collaring. Of 13 mortalities, two died of unknown causes, 10 were caught by trappers, and one died after 13 months from injuries related to the radio collar. One juvenile female was collared in March 1999 and monitored for 3 months before her collar signal disappeared.

There were significant effects of sex ($P < 0.001$, $F_{[1,23]} = 108.9$) and age class ($P < 0.05$, $F_{[1,23]} = 4.6$) on the mass of captured marten (Table 2). Males were larger than females, and adult marten were larger than juveniles.

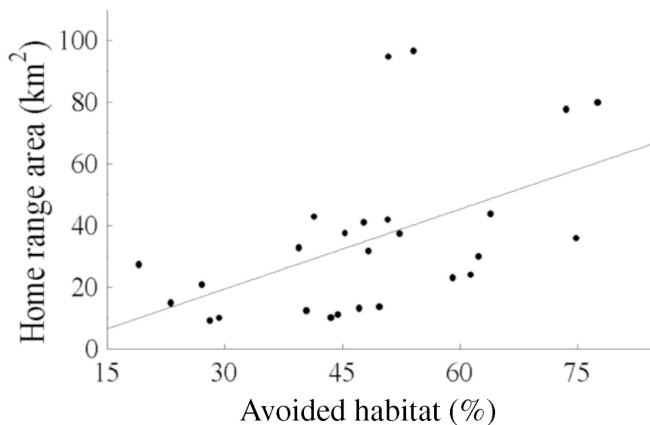
Between October 1998 and March 2000, 28 marten were radio-tracked for 11.6 ± 2.7 months, generating a total of 462 locations. Two animals, observed for <5 months each, were discarded from the analysis of annual home ranges. The mean error of locations for 14 test collars was 155.5 ± 112.2 m.

Small mammal abundance was high during the study. In 99 trap-nights per year, a total of 71 animals was trapped in

Table 3. Availability and use of habitats by American marten in southeastern Labrador.

Stand type	Number of locations	Proportion of total locations	Proportion of available habitat	Confidence limits on use
Burn	7	0.015	0.015	0.001–0.030
Bog*	23	0.05	0.082	0.024–0.076
Scrub forest*	176	0.381	0.463	0.322–0.439
Medium mixed	4	0.009	0.008	0.000–0.020
High mixed	6	0.013	0.005	0.001–0.026
Medium spruce–fir	52	0.113	0.09	0.075–0.150
High spruce–fir	90	0.195	0.157	0.148–0.242
Medium spruce	63	0.135	0.119	0.095–0.177
High spruce	41	0.089	0.061	0.055–0.123
Total	462	1.000	1.000	

*Confidence limits and significantly avoided habitat types are Bonferroni-adjusted (experimentwise $\alpha = 0.05$).

Fig. 2. Relationship between the proportion of avoided habitat types in the home range and home-range size for American marten in southeastern Labrador.

1998, and 74 animals in 1999. In 1998, 59 red-backed voles (*Clethrionomys gapperi*), 8 meadow voles (*Microtus pennsylvanicus*), and 4 masked shrews (*Sorex cinereus*) were captured. In 1999, 61 red-backed voles, 10 meadow voles, and 3 masked shrews were trapped.

Home range and habitat selection

Home-range size for all animals ($n = 26$) was 36.2 ± 25.5 km² (range = 9.2–96.6 km²). The value for 12 male marten was 45.0 ± 28.7 km² (range = 10.0–96.6 km²), and for 14 females, 27.6 ± 20.3 km² (range = 9.2–79.9 km²). Male home ranges were significantly larger than female home ranges (one-tailed test; $P < 0.05$, $F_{[1,23]} = 3.21$), but there was no significant effect of age ($P > 0.37$, $F_{[1,23]} = 0.82$) on home-range size. There was no significant correlation between the number of locations for individual marten and the size of their home ranges ($P > 0.42$, $r = -0.16$, $n = 26$).

Marten showed no significant preference for any habitat type, but they significantly avoided scrub forests and bogs, areas of no or low canopy cover ($P < 0.001$, $\chi^2 = 31.64$, $df = 8$; Table 3).

Home-range variation

Within our population, there was a significant positive relationship between the proportion of avoided habitat types in

the home ranges and the size of that home range ($P < 0.006$, $r = 0.52$, $F_{[1,24]} = 8.86$; Fig. 2). There was no significant effect of body mass on home range for males ($P > 0.43$, $r = 0.31$, $F_{[1,9]} = 0.69$) or females ($P > 0.46$, $r = 0.28$, $F_{[1,9]} = 0.62$).

We tabulated environmental conditions, body size, and home-range sizes for marten populations across North America (Table 4). There were no significant relationships of any of these potential influences with home-range size for either sex, i.e., of mean January temperature for males ($P > 0.52$, $r = -0.22$, $F_{[1,9]} = 0.42$) or females ($P > 0.32$, $r = -0.33$, $F_{[1,9]} = 1.1$), number of months of continuous snow cover for males ($P > 0.17$, $r = 0.44$, $F_{[1,9]} = 2.2$) or females ($P > 0.25$, $r = 0.37$, $F_{[1,9]} = 1.5$), or annual snowfall for males ($P > 0.52$, $r = 0.20$, $F_{[1,9]} = 0.44$) or females ($P > 0.43$, $r = 0.26$, $F_{[1,9]} = 0.69$).

Discussion

For marten in Labrador, the avoidance of areas with sparse canopy cover (<20%) is consistent with previous studies of marten at the stand scale (Bateman 1986; Strickland and Douglas 1987; Bowman and Robitaille 1998; Potvin et al. 2000). Beyond this pattern of avoidance, however, in our study there was no selection for particular stand characteristics such as species composition or higher degrees of canopy cover. Because of this lack of selection and the generally homogeneous nature of the forests (i.e., no stands were <50% coniferous content and nearly all stands were >80 years old), we surmise that all productive forest stands in the study site may be suitable for marten. In Labrador, marten habitat selection can be envisaged primarily as the use of dense canopy stands, isolated in a matrix of avoided scrub forests and bog.

Annual home ranges of 45 km² for males and 27 km² for females were appreciably larger than any previously reported for the species (Buskirk and McDonald 1989). The largest single home range published for American marten was 27.5 km² for a male in Newfoundland (Bateman 1986); the largest home range in our study was just under 100 km². Although the extremes in home-range areas in our study (9.2–96.6 km²) were exceedingly different, other studies have revealed within-population differences that span an order of magnitude (Buskirk and McDonald 1989; O'Doherty et al. 1997). The coefficient of variation (SD/mean) of the

Table 4. Home-range size, body size, and climatological data for populations of American marten in North America.

Location	Source(s)	Latitude (N), longitude (W)	Home-range estimator, % MCP	Mean January temperature (°C)	Months of snow cover	Mean annual snowfall (cm)	Mean mass (g)		Home-range size (km ²)	
							Male	Female	Male	Female
Northwest Territories	Latour et al. (1994)	65°15', 126°49'	100	-28.9	7	147	NP ^a	NP ^a	14.2	6.8
Alaska	Buskirk (1983) ^b	62°48', 148°50'	100	-20	7	378	1288	916	7.1	7.9
Yukon	Archibald and Jessup (1984) ^b	61°12', 133°20'	100	-18.7	7	149	1243	862	6.1	4.8
Labrador	This study	53°17', 57°20'	100	-13.8	7	440	1228	820	45	27.6
Manitoba	Raine (1981) ^b	51°06', 95°20'	100	-18	5.5	138	1225	660	11.1	12.5
Ontario	Thompson and Colgan (1987)	49°15', 85°35'	100	-17	6	310	NP	NP	5.2	3.2
Newfoundland	Bateman (1986) ^b	48°24', 57°40'	100	-5.7	6	411	936	681	27.5	17.7
Newfoundland	Bissonette et al. (1988) ^b	48°24', 57°40'	95	-5.7	6	411	1325	944	12.8	5.6
Quebec	Potvin and Breton (1997)	47°41', 78°16'	100	-17	6.5	317	937	631	8.9	9.5
Minnesota	Mech and Rogers (1977) ^b	47°42', 91°30'	100	-13.9	5.5	201	840	672	15.7	4.3
Maine	Steventon and Major (1982) ^b	45°30', 69°30'	100	-8.9	4.5	196	812	534	9.2	2.5
Maine	Katnik et al. (1994)	46°02', 69°09'	95	-8.9	4.5	196	NP	NP	5.2	2.8
Maine	Phillips et al. (1998)	46°02', 69°00'	95	-8.9	4.5	196	NP	NP	2.6	2
Wyoming	O'Doherty et al. (1997)	41°03', 106°45'	95	-10.6	7	138	NP	NP	16	6.3
California	Spencer (1981); Simon (1980) ^b	39°30', 120°20'	100	3.2	4	599	1002	668	3.9	3.2

^aNP = data not published.^bData from Buskirk and McDonald (1989).

home ranges for marten in Labrador was 70.5%, comparable with that from populations in Alaska (67.0%; Buskirk 1983) and New York (56.1%; Buskirk and McDonald 1989).

Labrador marten also exhibited sexual differences in home-range area. In our study, the ratio of male to female average home-range size was 1.7:1, similar to other populations (Strickland and Douglas 1987; Clark et al. 1989; Katnik et al. 1994; Latour et al. 1994). Although also sexually dimorphic in body size, we found no relationship between home-range size and body size in our population. Although this within-population relationship exists for some species (McLoughlin and Ferguson 2000), it had never previously been tested for marten. With respect to body mass, males and females in our study were comparatively large (Strickland and Douglas 1987), although in the range of what has been reported elsewhere in the taiga (Buskirk and McDonald 1989; Latour et al. 1994).

Space use by marten may be closely linked to prey abundance. During small mammal declines, marten home ranges tend to increase, and individuals tend to occupy highly variable home ranges, making identifying home-range size difficult (Thompson and Colgan 1987). However, the exceptionally large home ranges in our study do not appear to result from diminishing prey numbers. Small mammal populations remained high during the entire study (Smith 2001). On the other hand, home-range size within the population varied with the proportion of avoided, less productive, habitat types. This suggests that, at least on this scale, a home range that includes more suboptimal habitat must be larger to meet that individual's needs (McLoughlin and Ferguson 2000). In Labrador, the less productive forest stands harbour lower densities of the red-backed vole (Simon et al. 1998), an important prey species (Spencer 1981; Simon et al. 1999). A similar relationship existed for marten in a logged environment in the taiga of Québec (Potvin et al. 2000). Within populations, home ranges may be indirectly correlated to local variation in resource abundance, not only for marten (Thompson and Colgan 1987), but also for other species, including Townsend voles (*Microtus townsendii*; Taitt 1981) and black bears (*Ursus americanus*; Powell et al. 1997). In our study, observations on small mammal abundance were not habitat-specific. Further study is necessary to examine the relationships between habitat-specific prey densities and the home-range size and habitat preferences of marten.

The analysis of intraspecific variation among populations is another useful approach to generating knowledge. For marten, a previous synthesis (Buskirk and McDonald 1989) reported that mean home-range size covaried with mean female body mass, with no apparent relationship to climate, based on annual temperature ranges and latitude. Our analysis of mean January temperature, as well as the quantity and duration of snow cover, supported these results. However, when we augmented this synthesis with more recent studies, no relationship between body size and home-range area was evident for either sex. Such an allometric relationship (Harestad and Bunnell 1979) is strongest when examined across species and may be inversely related within the species (Ferguson and McLoughlin 2000).

McLoughlin and Ferguson (2000) identified habitat productivity or food availability as the primary determinant of home-range size within a species. Among populations, rela-

tionships between productivity or food availability and home-range size have been found in red squirrels (*Sciurus vulgaris*; Wauters and Dhondt 1992), black-throated blue warblers (*Dendroica caerulescens*; Wunderle 1995), and mule deer (*Odocoileus hemionus crooki*; Relyea et al. 2000), but further study is required to test this relationship for marten. The fact that more than 50% of the total area in our study consisted of avoided habitat types suggests that this factor may be important at scales beyond the individual and that further study is required.

Labrador forests are remarkable for their comparatively low productivity, as evidenced by very slow growth rates and large peatlands (Foster 1983). As our study highlights, Labrador marten may be equally remarkable. Their large requirements for space in a such a slow-growing forest environment suggest appreciable challenges to the management of marten and their habitat in Labrador.

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