THESIS

BEHAVIOR AND DISTRIBUTION OF

AMERICAN MARTEN (*MARTES AMERICANA)*

IN RELATION

TO SNOW AND FOREST COVER

ON THE KENAI PENINSULA, ALASKA

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS
PREPARED UNDER OUR SUPERVISION BY ANDREW P. BALTENSPERGER ENTITLED
**BEHAVIOR AND DISTRIBUTION OF AMERICAN MARTEN (*MARTES AMERICANA)*
IN RELATION TO SNOW AND FOREST COVER ON THE KENAI PENINSULA,
ALASKA** BE ACCEPTED AS FULFILLING IN
PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

BEHAVIOR AND DISTRIBUTION OF AMERICAN MARTEN
(*MARTES AMERICANA)* IN RELATION TO SNOW AND FOREST COVER
ON THE KENAI PENINSULA, ALASKA

Marten are sensitive to cold temperatures and normally rely on an insulating snow-pack and sufficient forest structure for thermal protection in winter. Low densities of marten on the western Kenai Peninsula, Alaska have commonly been attributed to shallow snow and habitat conditions that may not be conducive to supporting stable marten populations. This research examined the interactions between marten behavior in relation to available snow and habitat conditions at forest stand, home range, and landscape scales. Marten were radio-collared and back-tracked in three study areas in the Kenai Mountains and Kenai Lowlands to investigate habitat selection and the effects of snow conditions on the movement and resting behavior of marten. An aerial digital videography survey, supplemented by trapping, museum and Kenai National Wildlife Refuge (KENWR) records, was used to generate a minimum landscape distribution estimate of marten on the Kenai Peninsula. Videography detections were overlaid with Geographic Information Systems (GIS) layers for spruce-bark beetle damage and fire history on the Kenai Peninsula. We also tabulated the number of days marten were exposed to conditions in which the subnivean environment was not insulated from below freezing ambient temperatures. Trends in maximum snow depths were calculated by fitting regression lines to historic snow records at Kenai weather stations since 1931.

Results demonstrated that marten chose rest sites in structures that would maximize thermodynamic efficiency given the availability of insulating snow cover and warm resting structures. While traveling, marten selected snow and habitat types largely in proportion to their availability at the home-range scale. Movement paths were more tortuous through habitat patches with higher than average canopy densities. Aerial videography surveys detected 32 locations of marten and indicated that the distribution of marten has expanded into the Kenai Lowlands where marten had previously not been reported in any abundance since the beginning of the 20th century.

Detections occurred four times as frequently in a large post fire sere burned in 1947 in contrast to an area burned in 1969. Marten were detected in areas extensively damaged by spruce-bark beetles in just six instances and were twice as likely to be located outside of beetle-damaged areas. Average numbers of stress days were inversely related to elevation and the associated differences in snowfall associated with elevation. Analyses of regional maximum yearly snow depths indicated that maximum snow depths have been increasing by 0.29 cm/year in the Kenai Mountains, whereas trends have remained relatively constant in other regions of the Kenai Peninsula. Variations in available snow pack, forest maturity and the availability of resting structures may explain recent shifts in distribution at the landscape level.

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DEDICATION

This research is dedicated to my high school biology teacher, Mr. Don Weiss, who first inspired

me to study biology through the sharing of his love and fascination of nature, and who taught me

that "Bio is Life."

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INTRODUCTION

The Kenai Peninsula is currently undergoing major shifts in land-cover composition as a result of climate change including increased spruce-bark beetle outbreaks, a shifting fire regime, a rising treeline, and drying wetlands (Klein et al. 2005, Knowles et al. 2006, Skinner, et al. 2006, Dial and Berg 2007). Additionally, accumulated yearly snow depths may also be increasing in the Kenai Mountains at a rate of 0.29 cm/year (Chapter 2). These environmental trends are likely to have far-reaching implications for numerous species, not only on the Kenai Peninsula, but throughout the boreal forest as a whole. Understanding how the resource requirements and environmental constraints of a sensitive species like the American marten may be affected by these trends at different spatial scales is central in the efforts to maintain functionality of the broader ecosystem.

Habitat selection by marten varies when resting, foraging, and traveling, and at different spatial scales (Johnson 1980, Spencer et al. 1983, Bissonette et al. 1997, Nams and Bourgeois 2004). Third-order habitat-selection decisions (Johnson 1980) such as where to rest or forage are made at the micro-site scale and are likely based on snow cover, canopy closure, coarse-woody debris (CWD), and available prey (Bissonette et al. 1997). Second-order, or home range selection, is likely based less on individual forest stand components and more on a composite of forest types and landscape features at coarser scales (Johnson 1980, Bissonette et al. 1997). First-order selection refers to how a species is distributed across a landscape (Johnson 1980, Nams and Bourgeois 2004).

Marten on the Kenai National Wildlife Refuge (KENWR), Alaska prefer closed canopy

forests (>55%) of white spruce (*Picea glauca*) and mountain hemlock (*Tsuga mertensiana*) with numerous snags and downed logs with average diameters of 7.0 cm (Schumacher et al. 1989). The distribution of marten on the KENWR appears to have expanded from the Kenai Mountains westward into lowland areas where marten had not been documented in decades (Chapter 2). Only recently have marten been detected in the western Kenai Lowlands, where we hypothesize that shallow snow cover and cold temperatures there may combine to elevate levels of thermodynamic stress for marten.

Ample snow necessary for insulating resting sites may affect the distribution of marten on the KENWR. Marten typically require access via CWD to subnivean resting sites that are insulated by >15 cm of snow, especially when temperatures are below freezing (Taylor and Buskirk 1994, Brainard et al. 1995). Freshly fallen snow (density = 0.1 g/cm^3) at depths as low as 15 cm is adequate to buffer temperature fluctuations in the subnivean environment between –5°C and 0°C even as ambient temperatures drop well below freezing (Formozov 1965, Merritt 1984, Buskirk et al. 1988, Marchand 1982, 1987, Taylor and Buskirk 1994). However, as snow settles and melts, its density often increases, and the depth of snow required to insulate the subnivean zone (hiemal threshold) increases in proportion to the density of snow (Marchand 1982, 1987). Snow depths greater than 50 cm, regardless of their density, sufficiently exceed the hiemal threshold (Marchand 1987) and occur more frequently at higher elevations (Chapter 2).

Previous research has focused on selection of resting sites in relation to snow cover in Alaska and Wyoming (Buskirk 1984, Buskirk et al. 1989, Corn and Raphael 1992, Ruggiero et al. 1998). However, few studies on marten have incorporated analyses of continuous movement path data, where sinuosity can be used to represent time and foraging effort spent within specific habitat types (Benhamou 2004, Nams and Bourgeois 2004). In this research, we combine investigations of habitat selection at second and third order scales to compare selection behavior of marten in lowland spruce forests versus mountainous hemlock/spruce forests on the KENWR. We hypothesized that movement pathways of marten would be more tortuous through forest

stands containing denser canopies and higher levels of CWD as marten seek to maximize foraging efficiency and protection from predators.

Selection was examined at resting sites, at sampled points along marten tracks, as well as for continuous linear movement path data along the same tracks in an effort to identify environmental constraints that may account for wider landscape distribution patterns of marten on the Kenai Peninsula. Our primary objective was to identify snow and habitat conditions important to the survival of marten in an effort to explain recent distribution shifts of marten given the altered forest composition and weather pattern dynamics of climate change. We hypothesized that marten would choose resting sites in areas of deeper snow and closed-canopied forest in order to reduce thermodynamic costs, while showing little selection for specific land-cover types or snow conditions while traveling.

STUDY AREA

We conducted research in three study areas on the KENWR located on the Kenai Peninsula in south-central Alaska (Figure 1.1). Study areas were selected to coincide with known or probable marten populations and were chosen to represent the spectrum of climatic ecozones that occur on the KENWR. Study areas on the eastern side of the peninsula were located in the Kenai Mountains at Upper Russian Lake (26.7 km^2, $200 - 600$ m elevation) and in the Surprise Creek drainage (11.0 km^2, $150 - 450$ m). These sites supported some of the highest known densities of marten on the peninsula (Schumacher et al. 1989). The third area was located on the western peninsula lowlands in the Swanson River oil and gas fields (83.5 km^2, $60 - 125$ m) and supported an apparently incipient population of marten.

Vegetation on the western Kenai Peninsula is largely dominated by black spruce (*Picea mariana*) especially on the Kenai Lowlands, whereas white spruce (*P. glauca*) and small stands of western hemlock (*Tsuga heterophylla*) are found in more xeric, upland sites (Schumacher et al.

1989, Reynolds 1990). The western peninsula is characterized by colder, drier winters. Monthly winter temperatures at the Kenai Airport (10 m elevation) ranged from average lows of –14.7° C in January to average highs of 0° C in March between 1949 and 2007 (Asbhy 2008). Snow cover on the Kenai Lowlands is highly variable. Maximum yearly snow depths ranged from 0 cm to 152 cm between 0 m and 300 m elevation (McClure 2006, Ashby 2008).

The eastern side of the Kenai Peninsula is dominated by Sitka spruce (*P. sitchensis*) and Lutz spruce (*P. x Lutzii*) at low to mid elevations, whereas mountain hemlock (*Tsuga mertensiana*) stands generally form the treeline, which occurs at 250 m to 700 m elevation (Schumacher et al. 1989, Reynolds 1990). A spruce bark beetle (*Dendroctonus rufipennis*) infestation has dramatically reduced white spruce canopy cover and increased amounts of CWD in 429,000 ha across the Kenai Peninsula between 1989 and 2002 (Berg et al. 2006). Near treeline, stands of sub-alpine shrubs are common, especially alder (*Alnus sinuata*) and willow (*Salix* spp.) (Schumacher et al. 1989, Reynolds 1990). Alpine tundra generally dominates above 750 m (Schumacher et al. 1989). Winters in the mountains typically have warmer lows with more precipitation. Monthly winter temperatures at Moose Pass (215 m elevation) ranged from average lows of –14° C in January to average highs of 2° C in March between 1952 and 2004 (Asbhy 2008). Maximum yearly snow depths ranged between 88 cm to 207 cm above 300 m elevation in the mountains since 1951 (McClure 2006, Ashby 2008).

METHODS

Trapping and Immobilization

We live-captured marten in 48 x 15 x 15 cm Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, WI) baited with Magnum Call marten lure (Blackie's Blend, Glenmont, OH), meat, and grouse wings. We attached a 17 x 17 x 25 cm plywood nest box to each trap to provide thermal protection for marten during cold weather. We immobilized captured marten using 9

parts ketamine hydrochloride (18 mg/kg body mass; 100 mg/ml concentration) and 1 part

xylazine hydrochloride (2 mg/kg body mass; 100 mg/ml concentration) injected into the hip

muscle (Belant 1992, Bull et al. 1996, Wilbert et al. 2000, Kreeger 2002). We weighed and sexed

individuals, inserted passive integrated transponder (PIT) tags (Biomark, Inc., Boise, ID), and

fitted marten with VHF radio collars with a range of 3 – 5 km (Telemetry Solutions, Inc.,

Concord, CA).

Ground-tracking and Rest-Site Characterization

We used ground-based field surveys to assess habitat and snow-cover use and to

characterize resting sites during periods of snow-cover between January 2007 and April 2008.

Two field technicians used radio telemetry to locate and then back-track $\geq$1 marten per day to its

previous resting site. Telemetry was conducted during daytime hours when marten were most

often at rest, allowing for precise location of marten in resting sites. We used a variation in pulse

rates of transmitters to ascertain if marten were active, resting, or dead. We measured snow

depth, canopy closure and land-cover type every 30 minutes along marten tracks (Corn and

Raphael 1992, Bull et al. 2005). Routes traveled between sites were logged using GPS units with

5-m accuracy.

For each resting site, we recorded: 1) type of resting structure (log, snag, alder, tree

canopy, red squirrel (*Tamiasciuris hudsonicus*) midden pile (Corn and Raphael 1992), 2) habitat

type, 3) snow depth, and 4) canopy closure (Sherburne and Bissonette 1994) within a 5-m-radius

plot centered around resting-site entrances and at a control site 100 m away in a random direction.

Snow depth and canopy cover were measured at the entrance and at one point in each of the four

cardinal directions along the circumference of the 5-m circular plot centered on the resting site.

Our methods for capturing, handling, and studying marten were reviewed and approved by

Colorado State University's Animal Care and Use Committee (protocols 06-097A-01, 06-097A-

02).

Data points collected along tracks and linear track pathways were intersected with a

Geographic Information Systems (GIS) (ArcMap 9.3) land-cover layer to determine the

proportion of telemetry locations and distances traveled within each land-cover type. The land-

cover layer was digitized from 1-m resolution aerial photographs taken during 1996 – 1997 and

using a 20-m resolution vegetation map as a reference (O'Brian 2005). Resting site locations,

telemetry locations, and tracks were plotted to outline home-ranges for each marten using

minimum convex polygon methods (Burt 1943). We opted not to use kernel density estimators

because of accuracy issues associated when applying these methods to small sample sizes

(Seaman and Powell 1996).

Vegetation Sampling

During July 2007, we conducted surveys of vegetation to characterize coniferous forest

stands in circular plots within each of the three study areas following methods used by the Forest

Inventory Analysis (U.S. Department of Agriculture 2002). Ten randomly generated points were

each placed within hemlock, white spruce, and black spruce at both Surprise Creek and the Kenai

Lowlands, and 10 points were each placed in hemlock and Sitka/Lutz spruce at Upper Russian

Lake. We measured four primary variables: 1) average canopy closure, 2) amount of CWD, 3)

presence of squirrel middens at each plot, and 4) density of snags. The number of snags was

measured within circular plots of radius 11.28 m. We measured canopy closure for coniferous

tree cover using a spherical densiometer faced away from the plot center at both endpoints of

three 11.28-m transects centered across the plot following azimuths of 120˚, 240˚, and 360˚,

(Corn and Raphael 1992, USDA 2002). Within a circular subplot of radius 5.64 m, we counted

the number of middens along transects and visually estimated their percent cover. Occurrences of

CWD with dbh $\geq$10 cm were also recorded along each transect within the 5.64-m subplot.

Abundance of CWD was transformed to a log scale for analysis. We used one-way analyses of

variance (ANOVA) to identify average differences in forest stand composition between study

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areas and land-cover types. We used a chi-squared test to analyze the presence of squirrel

middens on plots.

Climatological Monitoring

To characterize snow cover within each study area, we established 19 snow and

temperature monitoring stations near roads and trails at predetermined elevations ranging from 90

– 425 m. We placed two iButtons™ (Maxim Integrated Products, Inc., Sunnyvale, CA) at each

station to record hourly air and subnivean temperatures at ground level. At the Discovery Well

hemlock station in the Lowlands, we also placed 2 iButtons in a squirrel midden pile at depths of

15 cm and 30 cm. We measured snow depths to the nearest cm with an avalanche probe at

established stations each day while working in a study area, and depths and densities at all

stations at the beginning of each month that snow was on the ground between February 2007 and

May 2008. Average snow-pack densities were measured by coring snow-packs with a 1.2-m-

length of 5-cm-diameter PVC pipe and weighing the contents with a spring scale to the nearest 5

g.

Habitat Selection Analyses

We determined selection of land-cover types by marten with compositional analyses

using individual marten as the experimental unit (Aebischer et al. 1993). Total area available for

the compositional analysis was tabulated for each land-cover type using the land-cover GIS layer.

The logarithm (logs) of the number of point locations along movement pathways and from radio

telemetry within a given habitat type were divided by the logs of the total number of locations for

each marten. Differences in log ratios between habitat types, weighted by the square root of the

number of locations for each animal, were compared with multivariate analysis of variance

(MANOVA) (Proc GLM, SAS Institute Inc., Cary, NC). We also performed the same analysis

using continuous linear movement pathway data instead of points sampled along the tracks.

Snow depths and canopy closures at resting sites were compared to paired control sites across study areas with paired t-tests (Proc TTEST, SAS Institute Inc. Cary, NC). Snow depths and canopy closures at resting sites were also compared to measurements along tracks to identify differences in selection based on specific behaviors of marten.

To estimate the amount of time marten spent in specific habitat types, we calculated the sinuosity for each linear pathway through a habitat patch. Sinuosity was calculated in a GIS by dividing the distance along each path by the Euclidean distance between the start and end points of the path (Benhamou 2004). Sinuosities were analyzed with ANOVA using a split-plot design, using the length of track segments as a covariate. Individual marten represented the experimental unit with multiple observations for each marten. Marten and marten*land-cover variables were included as random effects in the model. Because of small samples in the analysis of sinuosity, the land-cover types "ice" and "open" were pooled, but were left as separate types in the compositional analysis. Statistical results were evaluated using $\alpha = 0.05$.

RESULTS

Capture and Home-ranges

We captured 6 marten (5M/1F) 16 times during 1,281 trap-nights in the Kenai Lowlands, 4 marten (2M/2F) during 114 trap-nights at Upper Russian Lake, and 1 male marten twice during 79 trap-nights at Surprise Creek. We followed 70.5 km of marten tracks in the 3 study areas, recorded data at 294 discrete points along tracks and located 27 resting sites of 9 marten (Table 1.1). We were unable to locate resting sites for 2 individuals before we lost radio contact with them. Home-range areas did not vary ($F_{2,5} = 0.16$, $P = 0.860$) among the Lowlands ($\bar{x} = 3.87$ km^2, SE = 0.346, $n = 3$), Upper Russian Lake ($\bar{x} = 4.04$ km^2, SE = 1.840, $n = 4$), and Surprise Creek ($\bar{x} = 2.26$ km^2, $n = 1$) study areas. We excluded one outlier, a dispersing juvenile in the Lowlands that had a home-range area of 31.91 km^2.

Snow Selection

Marten did not rest at sites with deeper snow ($t_{24} = -1.07$, $P = 0.294$) or denser canopies ($t_{26} = 1.53$, $P = 0.139$) than at paired control sites in any of the three study areas at the 100 m scale (Table 1.2). Snow depths ($t_{18} = -0.02$, $P = 0.984$) and canopy closures ($t_{18} = 1.14$, $P = 0.267$) also did not vary between paired resting sites and locations along marten tracks in each study area (Table 1.3). Snow depths at resting sites varied among study areas ($F_{2,22} = 35.69$, $P < 0.001$). Snow was deeper at Upper Russian Lake ($P < 0.001$) than at resting sites in the Kenai Lowlands (Table 1.2) where marten frequently utilized alternative resting site structures that did not rely on snow for insulation. Snow depths at rest sites at Surprise Creek were shallower than at Upper Russian Lake ($P = 0.030$) but deeper than in the Lowlands ($P = 0.007$).

Snow depths along marten tracks also differed among all study areas ($F_{2,532} = 539.96$, $P < 0.001$) and were shallower in the Lowlands than at Upper Russian Lake ($P < 0.001$) and Surprise Creek ($P < 0.001$) (Table 1.3). Snow depths collected from 19 snow stations between January 2007 and April 2008 in the regions surrounding each study area showed that snow depths were deeper (Figure 1.2) and densities were greater in the mountains than in the Lowlands (Figure 1.3). Weather stations in the Lowlands and Surprise Creek study areas demonstrated that the subnivean zone is buffered from ambient temperatures only when snow-pack conditions surpass the hiemal threshold (Figures 1.4, 1.5). The iButton placed 15 cm deep in a squirrel midden recorded temperatures nearly equivalent to ambient temperatures when no snow was present. However, the iButton placed at a depth of 30 cm, did not record temperatures below –4.5˚ C while ambient temperatures fell as low as –20˚ C.

Habitat Selection

Of the 7 instances marten were found resting in the Lowlands, 3 were located in squirrel midden piles, 1 in an underground burrow and 3 in tree canopies (Table 1.4). We did not find marten resting under snow-covered logs, alders or snags in the Lowlands, whereas the 18 resting

sites at Upper Russian Lake and two sites at Surprise Creek were all located under snow-covered structures (Table 1.4). Resting sites in the Lowlands were found exclusively in white spruce forest, whereas hemlock stands at Upper Russian Lake contained the most resting sites (Table 1.5).

Canopy closure above tracks in the winter varied among study areas ($F_{2,480} = 6.37$, $P = 0.002$) and was highest at Upper Russian Lake (Table 1.3). Available canopy closures on random plots surveyed in the summer differed among study areas ($F_{2,72} = 16$, $P < 0.001$), and were lower at Surprise Creek than at Upper Russian Lake ($P < 0.001$) and in the Lowlands ($P = 0.011$). Overall abundance of all species of CWD on 100 m^2 vegetation plots surveyed in the summer did not differ among study areas ($F_{2,72} = 3.01$, $P = 0.055$), but levels of white/Lutz spruce CWD were greater at Surprise Creek than levels of white/Lutz spruce CWD in the Lowlands ($P < 0.001$) and at Upper Russian Lake ($P = 0.048$) (Table 1.6). Squirrel middens occurred on 1.8 times as many random plots in the Lowlands as at Upper Russian Lake and on 3.7 times as many plots as at Surprise Creek ($X^2_2 = 0.045$). The proportion of plots that contained squirrel middens did not vary by vegetation type ($X^2_2 = 0.141$).

Movement pathways of marten were more sinuous through denser forests ($F_{4,27} = 42.98$, $P < 0.001$) like hemlock and white/Lutz spruce stands in comparison to those through black spruce and deciduous stands (Table 1.7). Alder patches contained pathways that were less sinuous than through hemlock stands ($P = 0.026$) but were not less sinuous than those through white/Lutz spruce stands ($P = 0.576$). Paths through open/ice-covered areas were substantially less tortuous than in any of the vegetated habitat patches ($P < 0.001$).

The overall compositional analysis demonstrated disproportionate selection of land-cover types ($F_{6,4} = 7.62$, $P = 0.035$), but did not detect differences in selection of land-cover types among study areas ($F_{12,4} = 1.09$, $P = 0.514$) using the number of points measured along marten tracks. Ice-covered water was the only land-cover type selected less than its availability ($P < 0.001$). Using linear movement pathways in the analysis, overall tests did not show

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disproportionate selection by land-cover types ($F_{6,3} = 5.18$, $P = 0.103$) or differences in selection of land-cover types among study areas ($F_{12,2} = 2.02$, $P = 0.379$). Home-ranges in the Lowlands and at Surprise Creek were comprised predominantly of white/Lutz spruce, whereas hemlock comprised a larger proportion of home-ranges at Upper Russian Lake (Table 1.5).

DISCUSSION

Marten showed dramatic differences in selection of types of resting sites between mountain and lowland areas on the Kenai Peninsula. Due to their long, slender bodies, low fat reserves, poorly insulative fur, high metabolic requirements, and lack of hibernation, marten are physiologically ill-equipped to cope with heat-loss at low temperatures (Buskirk et al. 1988, Buskirk and Harlow 1989). In areas where snow conditions are deep enough for the hiemal threshold to be met, selecting resting sites that take advantage of the insulating properties of snow is one of the most efficient ways for marten to buffer against cold ambient temperatures (Spencer et al. 1983, Buskirk 1984, Bateman 1986, Corn and Raphael 1992, Wilbert et al. 2000). However, our data indicate that red squirrel middens may provide viable resting alternatives to subnivean sites, especially in the absence of snow-cover (Buskirk 1984, Buskirk et al. 1989, Sherburne and Bissonette 1993). Marten in the Lowlands did not rest under snow when it was available, likely because it did not occur at depths that exceeded the hiemal threshold.

In mountain areas where snow exceeding the maximum hiemal threshold (>50 cm) was readily available, marten rested exclusively under the snow in spaces around the bases of trees and under logs in our study areas and elsewhere (Buskirk 1984, Spencer 1987, Buskirk et al. 1988, Sherburne and Bissonette 1993). We did not document marten using squirrel middens in the mountains, although middens were available and appear to be a thermodynamically efficient alternative to snow-covered resting sites (Buskirk 1984, Ruggiero et al. 1998, Pearson and Ruggiero 2001). In this case, squirrel middens likely represented an unnecessary resting site alternative, given the abundance of snow and the difficulty of accessing them beneath the snow.

Deep snow which frequently exceeded 50 cm and ensured the thermal efficiency of most

potential resting sites in the mountains could explain why marten did not select snow depths at

resting sites significantly different from depths at control sites. The similarity of snow conditions

between resting and control sites however, represents a lack of discrimination only at the fine

100-m scale at which conditions were measured.

In contrast, snow along marten tracks averaged 36.4 cm and just 26.5 cm at control

resting sites in the Kenai Lowlands. These depths, combined with average snow densities

between 0.15 and 0.33 g/cm^3, were often not sufficient to meet the hiemal threshold and therefore

snow generally did not represent a beneficial resting medium there (Figure 1.3). Instead, marten

used alternative resting site structures such as squirrel middens to overcome environmental

conditions that were on average, more stressful than at higher elevations in the mountains

(Chapter 2). Our results are similar to other research in Alaska. Of 37 winter resting sites found

by Buskirk (1984) in south-central Alaska, 26 were located in red squirrel midden piles, all but

two of which were active. In contrast, the use of middens by marten in the contiguous United

States averaged <10% of total resting site use (Pearson and Ruggiero 2001). These results may

point towards a unique resting strategy utilized by marten in regions like Alaska where very cold

temperatures are often combined with shallow snow cover. Squirrel middens were more readily

available for use in the Kenai Lowlands than in the Kenai Mountains (Table 1.4), but given the

lack of insulating snow cover, we believe their more frequent use there occurred more out of

necessity than opportunity. Because of more variable temperatures, winter rain events, and the

correspondingly unreliable snow-pack in the Kenai Lowlands, marten there cannot always depend

on snow to provide them with insulated resting sites. More stable temperatures in the mountains

prevent the degree of melting and snow-pack degradation, and snow depths that normally exceed

50 cm are more than sufficient to insulate resting marten at any density of snow throughout the

winter (Marchand 1987).

Snow depths along marten tracks were similar to those at resting sites in each of the three

study areas. Marten do not appear to be restricted by snow conditions while moving, because they have one of the lowest foot-loading weights of all carnivores (Formozov 1965, Raine 1986). Marten tracks in all 3 study areas rarely sank > 5 cm into the snow, lending support to this notion.

The selection of canopy densities by marten at resting sites and along tracks did not indicate a preference for canopies that differed from those available within study areas. Marten generally utilize mature, old-growth conifer forests with a closed canopy cover >50% (Spencer et al. 1983, Snyder and Bissonette 1987, Koehler et al. 1990, Corn and Raphael 1992, Buskirk and Ruggiero 1994). Our data show average selection of canopy density to be somewhat less than that previously reported. This may be the result of a reduction in available overhead cover caused by spruce bark beetle outbreaks on the KENWR where average forest canopy closure is 42% (Barrett 2008).

While the overall compositional analyses showed only an aversion of marten for ice covered bodies of water, the sinuosity analysis, on the other hand, indicated that marten were spending more time in hemlock and white spruce forests. The higher use of these forest types may be due to their denser canopies, elevated levels of CWD, and higher densities of squirrel middens when compared to the other available vegetated land-cover types. More tortuous paths may also reflect increased foraging effort in those land-cover types where higher densities of CWD would provide more subnivean entrances to investigate. Alternatively, higher sinuosities could also indicate a decrease in the efficiency of travel through forest types as a result of marten needing to circumnavigate obstacles on the forest floor. The nearly straight-line paths marten took across open areas support the notion that marten avoid crossing open areas in favor of the protection, superior foraging, and increased resting opportunities available in forest stands containing ample CWD, middens, and closed overhead canopies (Spencer et al. 1983, Snyder and Bissonette 1987, Koehler et al. 1990).

The forest types of hemlock and white spruce, through which marten paths were most sinuous, comprised large proportions of home-ranges. Establishing home-ranges in areas with

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sufficient snow cover, on the other hand, may be of less importance than arranging them around

suitable forest stands. While marten are likely found in higher densities in mountainous areas

with higher annual snowfalls, their occurrence in areas such as the Kenai Lowlands is testament

to their adaptive nature. While marten did not select for specific habitat or snow conditions at the

100-m third-order scale, their utilization of alternative, yet sufficiently insulating resting sites in

the Kenai Lowlands has allowed them to overcome thermodynamic limitations which might have

precluded them from inhabiting these low-elevation areas.

Management Implications

Trends in forest composition and snow conditions related to climate change pose

significant challenges for wildlife managers as they aim to conserve marten populations on the

KENWR and elsewhere. Because of thermal constraints imposed by winters in Alaska, the

distribution of marten on the KENWR may be limited to habitat that meets certain minimum

standards for available resting sites, midden piles, forest cover, CWD, and to a lesser extent snow

(Spencer et al. 1983, Schumacher et al. 1989). An abundance of squirrel middens in areas lacking

sufficient snow cover, or alternatively snow depths >15 cm, could be important for maximizing

marten energy conservation and survival (Buskirk et al. 1989, Schumacher et al. 1989). Recent

snow analyses indicate that maximum yearly snow depths have been increasing in the Kenai

Mountains and have remained relatively constant across the rest of the Kenai Peninsula over the

past 77 years (Chapter 2)**,** however it will be worth monitoring whether these trends hold into the

future given the predictions forecasted with a warming climate.

With the increasing intensities of beetle outbreaks and a shifting fire regime, the potential

for habitat regime changes capable of affecting marten is substantial. Beetle damage has already

reduced overhead canopies especially on the western Kenai Peninsula. White spruce seedling

recruitment after beetle damage has been shown to be adequate to restore forests to pre-outbreak

densities of white spruce, however seedling recruitment was also negatively associated with

Calamagrostis sp. grasses (Boggs et al. 2008). If white spruce seedlings are successfully excluded by *Calamagrostis* sp. grasses or if post-fire seres are converted to early-successional, hardwood forests, marten may find these areas less suitable (Chapin et al. 1997, Matsuoka et al. 2001, Payer and Harrison 2003). While snags and downed trees in beetle-killed white spruce forests may initially provide adequate cover for marten, as CWD decays, marten may find it increasingly difficult to find warm resting sites there. The chief prey of marten, voles and red squirrels, may also not survive well in these areas (Koprowski 2005, McDonough and Rexstad 2005). A reduction in red squirrel and midden densities could dramatically limit the availability of alternative resting sites for marten that are vital in the absence of an insulating snow layer.

Wildlife managers should be cognizant of the potential for elevated thermodynamic stress levels exerted on marten and their prey in a given winter, especially at low elevations. During years where snow conditions do not meet the hiemal threshold for a large proportion of the fall and early winter seasons, managers might consider restricting marten harvests in areas with limited snow cover or low densities of potential resting sites. Adequate resting and foraging opportunities are vital to marten population persistence, and their availability should be considered when establishing harvest regulations. Managers should evaluate conditions annually in an effort to conserve marten while they endeavor to better understand the effects of constraining factors within the context of the changing environment.

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Table 1.1 Number of locations and total length of tracks comprising home-ranges of individual marten in 3 study areas on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007–08.

Study area	Sex	Home-range area (km^2)	Locations (n)	Total track length (km)
Lowlands	F	31.91	33	8.737
Lowlands	M	3.20	11	0.783
Lowlands	M	4.06	12	3.471
Lowlands	M	4.35	70	15.907
Upper Russian Lake	F	0.39	15	1.155
Upper Russian Lake	M	6.04	63	6.790
Upper Russian Lake	M	8.17	19	3.454
Upper Russian Lake	F	1.54	21	4.601
Surprise Creek	M	2.27	29	3.471

Table 1.2 Average snow depth and canopy closures at resting sites and control sites 100 m away in three study areas on the Kenai Peninsula, Alaska during the winters of 2007 and 2007–08.

| Study area | n | Snow depth (cm) | | | | Canopy closure (%) | | | |
| | | Resting sites | | Control sites | | Resting sites | | Control sites | |
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lowlands	7	15.44	7.17	26.52	2.83	52.71	7.08	39.74	6.73
Surprise Creek	2	81.50	0.10	96.40	0.80	17.00	7.00	0.19	2.50
Upper Russian Lake	18	127.12	6.83	135.14	14.73	41.77	6.52	32.07	8.06

Table 1.3. Snow depth and percent canopy closure measured at points along marten tracks every 30 minutes in three study areas on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007–08.

Study Area	Snow Depth (cm)			Canopy %		
	n	$\overline{x}$	SE	n	$\overline{x}$	SE
Lowlands	149	36.39	1.40	127	33.09	2.48
Surprise Creek	19	85.30	11.45	10	9.50	7.86
Upper Russian Lake	130	146.33	4.93	131	42.60	3.31

Table 1.4. Types of structures used as resting sites by marten and the availability of each structure type in three study areas on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007–08.

Study Area	Resting site type	Resting sites used	Resting site availability[a]	
		n	$\bar{x}$	SE
Lowlands	CWD[b]	0	2.97	0.54
	snag	0	1.80	0.37
	midden[c]	3	37.50	
	tree	3	22.30	2.17
	underground	1		
Upper Russian Lake	alder [d]	9	4.06	
	CWD[b]	6	27.90	3.08
	snag	2	2.85	0.36
	midden[c]	0	20.00	
	tree	0	27.9	3.08
Surprise Creek	alder [d]	1	0.22	
	CWD[b]	1	6.23	1.10
	snag	0	3.83	1.10
	midden[c]	0	10.00	
	tree	0	22.53	2.50

[a]Mean occurrence of resting site structures occurring on circular vegetation plots (100 m^2).
[b]Occurrences of coarse-woody debris
[c]Percentage of plots surveyed containing ≥ 1 squirrel midden
[d]Occurrences of alders were not recorded on study plots. Total area (km^2) within home-ranges in each study area is used instead.

Table 1.5. Land-cover classification for resting sites used by marten during the winters of 2007 and 2007–08 and the % area available within the combined home-ranges in each study area on the Kenai National Wildlife Refuge, Alaska, USA.

Study Area	Land-cover	Resting sites (*n*)	Home-range % area[a]
Lowlands	white spruce	7	60.88%
	hemlock	0	1.13%
	black spruce	0	20.84%
	alder	0	0.13%
	deciduous	0	0.21%
Upper Russian Lake	hemlock	11	40.95%
	Lutz spruce	5	13.13%
	alder	1	25.15%
	deciduous	1	0.31%
	black spruce	0	
Surprise Creek	hemlock	1	21.62%
	Lutz spruce	1	67.95%
	black spruce	0	0.88%
	alder	0	17.91%
	deciduous	0	2.21%

[a]Sum of each land-cover area within marten home-ranges divided by the total area of home ranges in each study area.

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Table 1.6. Mean available forest stand metrics measured on random circular vegetation plots (100 m^2) for three dominant land-cover types in each of three study areas on the Kenai Peninsula, Alaska, USA during the summer of 2007.

Study area	Variable	white/Lutz spruce		hemlock		black spruce	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lowlands	canopy (%)	52.00	4.87	89.2	3.94	67.0	4.27
	CWD (#)	3.80	1.08	3.10	1.08	2.00	0.56
	middens[a] (%)	29.17		2.00	0.84	44.44	
	snags (#)	1.20	0.53	3.30	0.59	0.90	0.54
Surprise Creek	canopy (%)	36.01	4.71	76.01	1.91	49.94	4.14
	CWD (#)	12.90	1.51	3.60	0.97	2.20	0.94
	middens[a] (%)	37.50		40.00		55.56	
	snags (#)	4.30	1.02	4.70	1.45	2.50	1.17
Upper Russian Lake	canopy (%)	62.62	4.68	91.10	1.91		
	CWD (#)	7.20	1.58	2.70	0.70		
	middens[a] (%)	37.50		40.00			
	snags (#)	3.60	0.56	2.10	0.35		

[a] Percentage of plots surveyed in study area containing squirrel middens.

Table 1.7. Sinuosity and length of movement pathways averaged by land-cover type across study areas and marten on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007–08.

Land-cover	n	Sinuosity $\bar{x}$	SE	Track length (m) $\bar{x}$	SE
hemlock	97	1.62 A	0.123	148.78	27.97
white/Lutz spruce	202	1.52 A	0.071	176.73	25.43
black spruce	73	1.32 B	0.086	75.58	11.08
alder	64	1.31 B*	0.101	58.57	11.26
open	55	1.17 C	0.067	27.74	4.68

[a] Estimates with different letters are significantly different at $\alpha = 0.05$.

* Alder was not found to be significantly different from hemlock, white/Lutz spruce or black spruce because of its relatively large standard error.
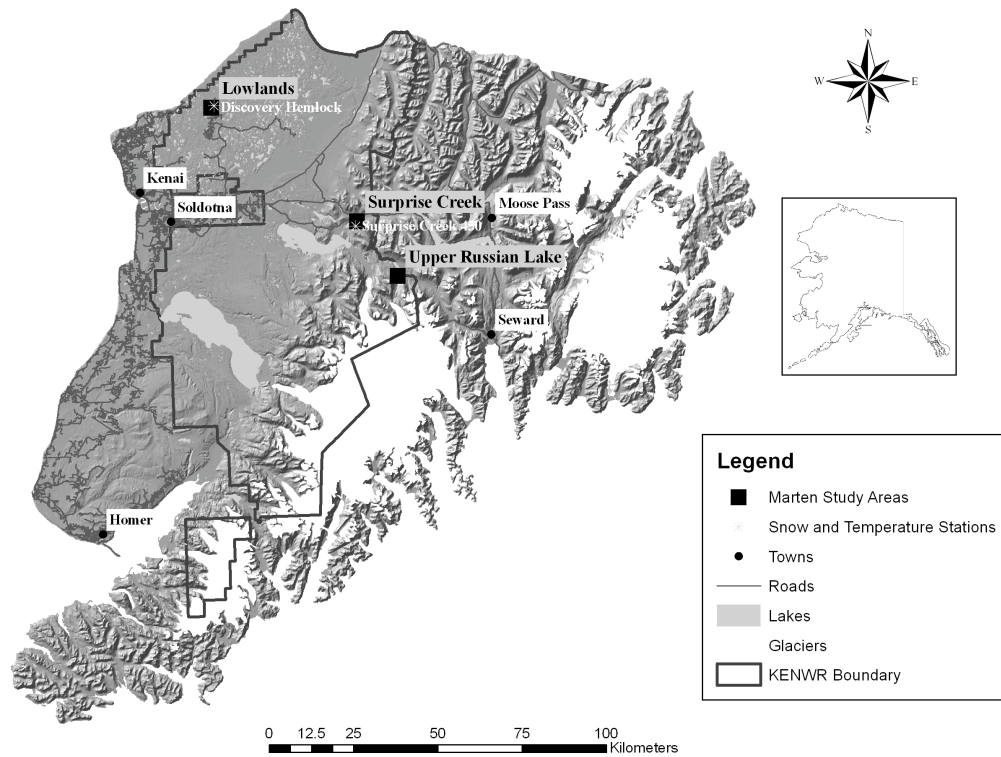
Figure 1.1. Marten study areas, Lowlands, Surprise Creek, and Upper Russian Lake, and two weather stations located on the Kenai National Wildlife on the Kenai Peninsula in south-central Alaska, USA during the winters of 2007 and 2007–08.
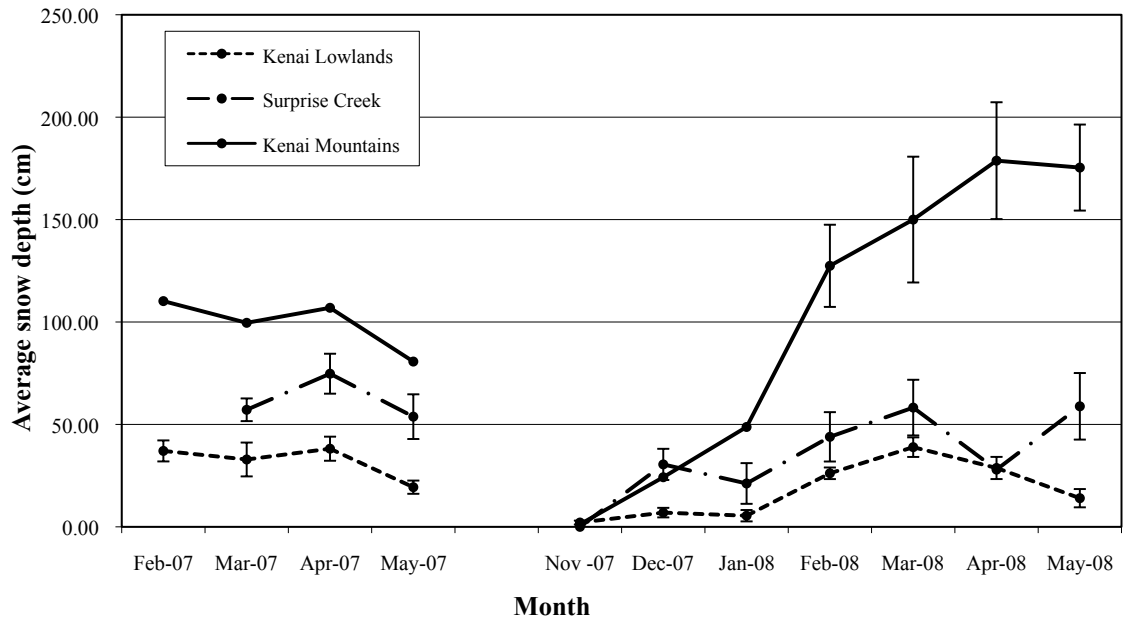
Figure 1.2. Monthly snow depths averaged across weather stations in three study areas on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007–08.
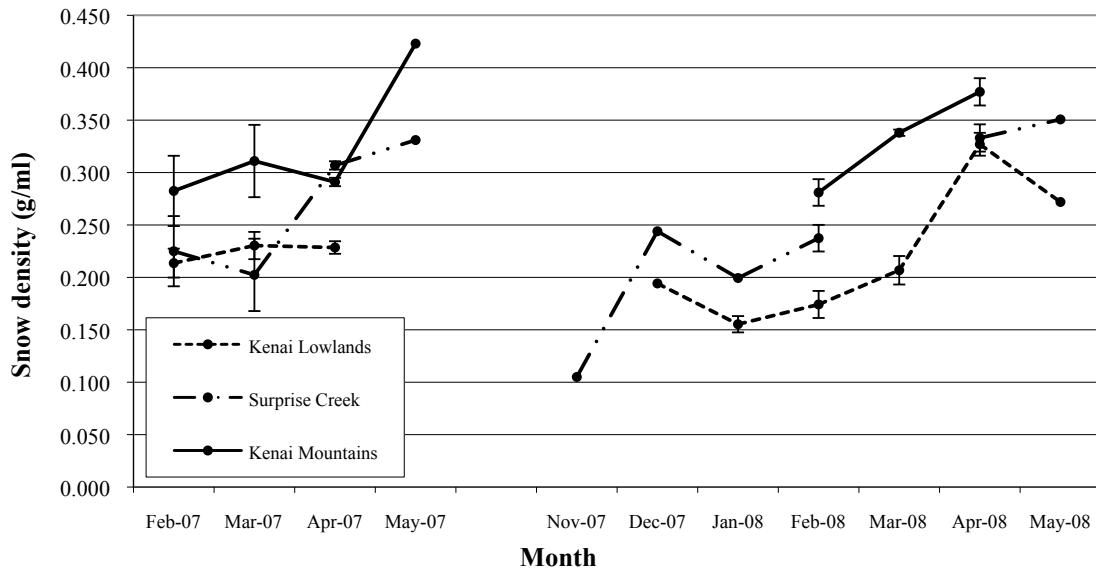
Figure 1.3. Monthly snow densities averaged across weather stations in three study areas on the Kenai Peninsula, Alaska, USA during the study period winters of 2007 and 2007–08.
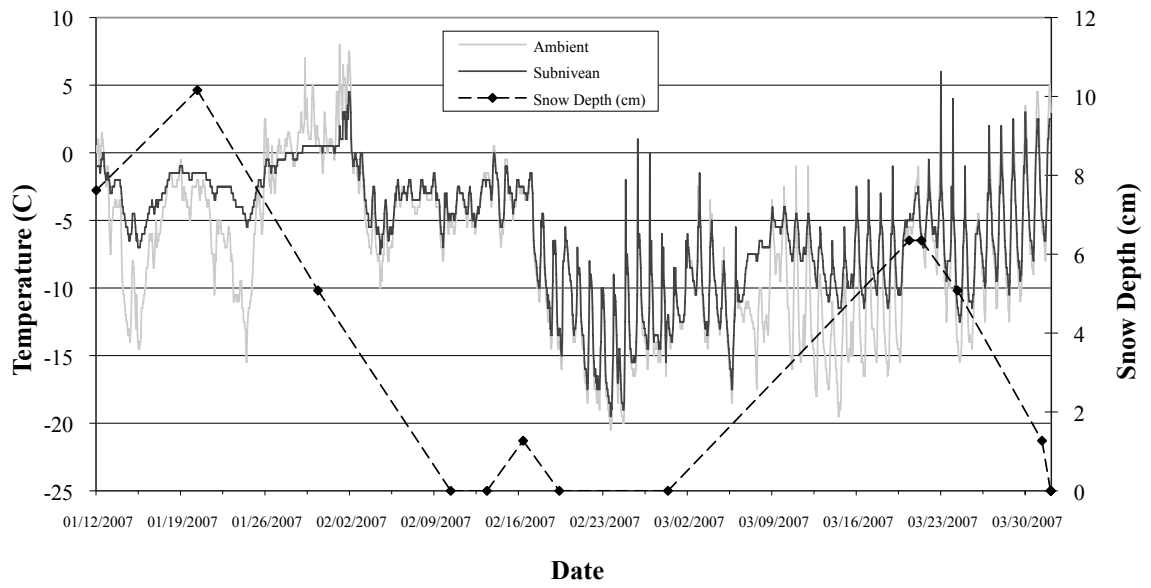
Figure 1.4. Subnivean and ambient temperatures in relation to snow depth at a weather station in a dense canopy hemlock stand at 90 m elevation in the Kenai Lowlands on the Kenai Peninsula, Alaska, USA during Winter 2007.
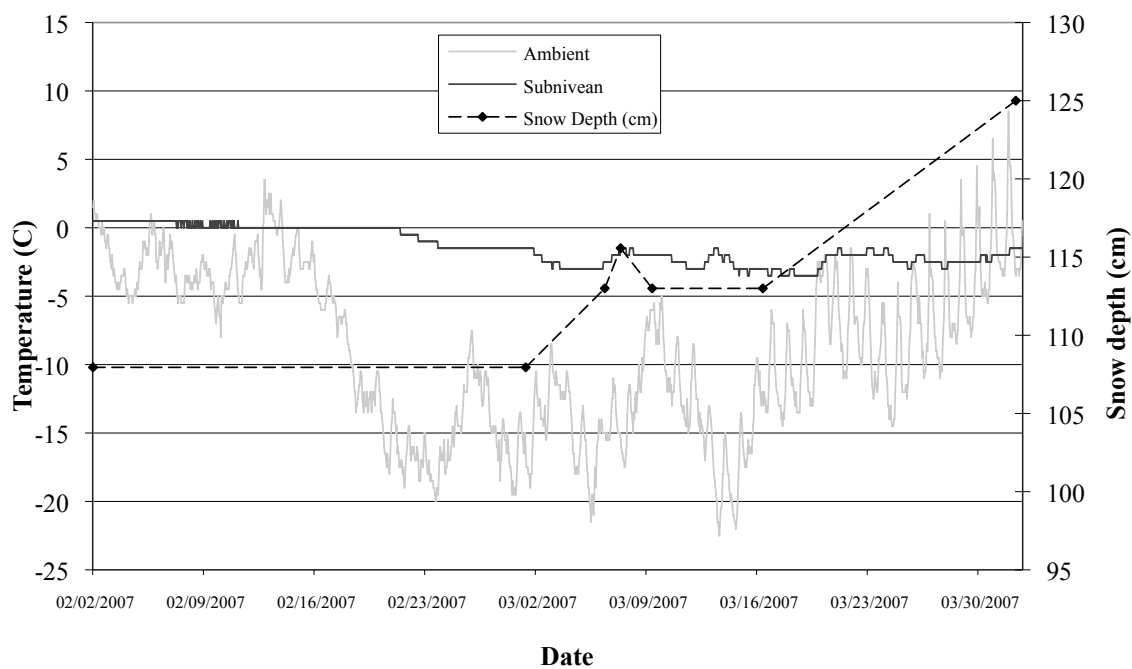
Figure 1.5. Subnivean and ambient temperatures in relation to snow depth at a weather station in an open white spruce/hemlock stand near treeline at 450 m elevation at Surprise Creek in the Kenai Mountains on the Kenai Peninsula, Alaska, USA during Winter 2007.

CHAPTER 2: DISTRIBUTION OF AMERICAN MARTEN (*MARTES AMERICANA)* IN RELATION TO SNOW COVER AND CLIMATE CHANGE ON THE KENAI PENINSULA, ALASKA, USA

INTRODUCTION

The Kenai Peninsula of Alaska has recently emerged at the forefront of issues on global climate change (DeVolder 1999, Berg 2005, Klein et al. 2005, Berg et al. 2006, Dial et al. 2007). Determining how to effectively manage wildlife populations within the context of a changing environment is becoming a paramount issue for conservation agencies. Because of their physiological sensitivity to environmental conditions, American marten (*Martes americana*) represent one of the most proximate, mammalian sentinel species of climate change (Weaver et al. 1996, Zielinski et al. 2005, Yom-Tov et al. 2008). The combination of a sensitive species inhabiting an area especially affected by climate change provides an excellent opportunity to document the associations between climate change and shifting wildlife distributions. Effective conservation of marten on the Kenai National Wildlife Refuge (KENWR) and throughout the boreal forest depends on accurate knowledge of their environmental and geographic constraints in relation to the availability of suitable habitat.

Average temperatures in Alaska over the past 50 years have increased by about 2° C, minimum winter temperatures have increased by almost 4° C, nearly 4 times that of summer temperatures, and the growing season has been extended by more than 14 days in spring (Hughes 2000, Berg 2005, Yom-Tov and Yom-Tov 2005). A 3° C change in mean annual temperature corresponds to an equivalent shift of 300 – 400 km in latitude or a 500-m change in elevation (Hughes 2000). Correspondingly Parmesan and Yohe (2003) reported a global average northward movement of 6.1 km per decade for a variety of terrestrial species. Rising treelines and the upward movement of sub-alpine plant species have been reported in western North

America and the European Alps (Peterson 1994, Pauli et al. 1996, Henry et al. 2006). Recent studies on the Kenai Peninsula have indicated a widespread rise in treeline of 10.1 m/decade, (Dial et al. 2007), a doubling in the relative area of black spruce (*Picea mariana*) forest over the past 50 years and a trend toward drier community regimes over the past 35 – 70 years (Klein et al. 2005).

A 30% increase in precipitation has been documented for much of Alaska (National Assessment Synthesis Team 2000) and an increase in the amount of rainfall at the expense of snowfall has been a predominant trend for the western United States over the past 50 years (Knowles et al. 2006). If a trend towards more rainfall in winter applies to the Kenai Peninsula, this could limit the extent of consistent, insulating snow cover during the winter. Elevated winter temperatures would also result in more frequent thaws, increasing the density of an already shallow snow-pack and reducing its ability to insulate subnivean (under the snow) species.

Trends toward increased forest area resulting from a drier climate could be conducive to facilitating an expansion in the distribution of marten. However, these potential gains in habitat area are contrasted sharply by damage to mature white spruce (*P. glauca*) forests, by a spruce-bark beetle (*Dendroctonus rufipennis*). Warmer summer temperatures and less frequent extreme low temperature events in winter have reduced the cold-related mortality of spruce bark beetles, and have led to shorter generation times and an increase in population growth rates (Logan et al. 2003, Berg 2005). On the Kenai Peninsula, a spruce bark beetle outbreak that has persisted since the mid-1980s has dramatically reduced white spruce canopy cover and increased amounts of coarse-woody debris (CWD) in 429,000 ha across the peninsula (Holsten et al. 1995, Berg and Anderson 2006).

The number of wildfires and their total burned area in western boreal Canada has nearly tripled since 1980 and appears to coincide with increasingly warm winter Pacific Ocean temperature cycles (Skinner et al. 2006). On the Kenai Peninsula, mean fire-return interval ranges between 400 and 600 years in white spruce forests and averages 79 years for black spruce

(De Volder 1999, Berg and Anderson 2006). Two fires in the last century burned large portions

of the Kenai Lowlands in 1947 (125,506 ha) and 1969 (34,818 ha) and fire frequency may be

increasing as a result of warmer summer temperatures (Morton et al. 2005).

Marten have strict physiological requirements in winter and it has been hypothesized that

the distribution of marten on the KENWR may be limited to habitat that meets minimum

insulating snow-pack conditions or areas with available insulating resting sites (Schumacher et al.

1989, Chapter 1). The depth of snow required to insulate the subnivean zone, or hiemal

threshold, insulates marten and their prey from below-freezing ambient temperatures while in

subnivean resting sites (Buskirk 1984, Marchand 1982, 1987, Taylor and Buskirk 1994, Brainard

et al. 1995). As the density of snow increases, particularly after thaw or winter rain events, the

minimum snow depth required to insulate the subnivean space may exceed 30 cm – 50 cm

(Formozov 1965, Marchand 1982, 1987, Halfpenny and Ozanne 1989). In areas at low elevations

like the Kenai Lowlands, that often lack an insulating layer of snow, marten were found to use

alternative sites, such as squirrel (*Tamiasciurus hudsonicus)* middens, which, at depths of 30 cm

or more, are sufficient to insulate marten from low temperatures even in the absence of snow

cover (Buskirk 1984, Spencer 1987, Buskirk et al. 1988, Sherburne and Bissonette 1993, Chapter

1).

Schumacher et al. (1989) concluded that a large population of marten inhabited the

eastern side of the Kenai Peninsula, but marten west of the Kenai Mountains were considered

extremely rare (Figure 2.1). Recent reports indicate that marten probably expanded into areas

where they had not been reported in decades. Using aerial digital videography tracking methods,

we aimed to estimate the minimum current distribution of marten at the landscape, or first order,

scale of selection (Johnson 1980) on the Kenai Peninsula, in relation to historic distributions and

landscape level processes associated with climate change.

Contemporary videography detections were overlaid with fire history and extent of

beetle-damage for the Kenai Peninsula. This research represents one of the first applications of

aerial digital videography technology for examining the distribution of mammals across a landscape. We hypothesize that while elevated levels of CWD may provide marten with an abundance of resting sites, the corresponding reduction in canopy closure resulting from beetle damage may result in a decrease of quality habitat for marten. Similarly, post-fire seres may also fail to provide marten with sufficient canopy coverage, while also limiting the amount of CWD available to marten for use as resting sites.

STUDY AREA

Research was conducted on the KENWR located on the Kenai Peninsula (152.053° E, 59.123° N; –148.816° E, 61.024° N; 0 – 1800 m elevation) in south-central Alaska. Vegetation on the western Kenai Peninsula is largely dominated by black spruce (*P. mariana*) especially on the Kenai Lowlands, whereas white spruce and small stands of western hemlock (*Tsuga heterophylla*) are found in more xeric, upland sites (Schumacher et al. 1989, Reynolds 1990). The western peninsula is characterized by colder, drier winters. Monthly winter temperatures at the Kenai Airport (10 m elevation) ranged from average lows of –14.7° C in January to average highs of 0° C in March between 1949 and 2007 (Asbhy 2008). Snow cover on the western Kenai is highly variable. Maximum yearly snow depths ranged from 0 cm to 152 cm between 0 m and 300 m elevation (McClure 2006, Ashby 2008).

The eastern side of the Kenai Peninsula is dominated by the Kenai Mountains where forests are comprised of Sitka spruce (*P. sitchensis*) and Lutz spruce (*P. x Lutzii*) at low to mid elevations, whereas mountain hemlock (*Tsuga mertensiana*) stands generally form the treeline (250 – 700 m) (Schumacher et al. 1989, Reynolds 1990). Near treeline, stands of sub-alpine shrubs, especially alder (*Alnus sinuata*) and willow (*Salix* spp.), are common (Schumacher et al. 1989, Reynolds 1990). Alpine tundra generally dominates above 750 m (Schumacher et al. 1989). The Kenai Mountains typically receive more precipitation and exhibit less daily

temperature variation in winter than in the lowlands. Monthly winter temperatures at Moose Pass (215 m elevation) ranged from average lows of –14° C in January to average highs of 2° C in March between 1952 and 2004 (Asbhy 2008). Yearly maximum snow depths in the mountains ranged between 88 cm – 207 cm above 300 m elevation since 1951 (McClure 2006, Ashby 2008).

METHODS

Historical Surveys

We compiled records of historic marten occurrences from four main sources: museum records, Alaska Department of Fish and Game (ADF&G) sealing records, KENWR furbearer records (reports, surveys and personal interviews with area trappers), and a KENWR marten research project (Schumacher et al. 1989), the only other study to examine marten distribution on the Kenai. We reviewed museum collections from the University of Alaska-Fairbanks and the University of California-Berkeley and recorded dates and locations of marten harvested and observed on the Kenai Peninsula since 1905. Personal interviews were conducted between January 2007 and April 2008 with area trappers and long-time residents to supplement a trapper survey conducted by Bailey in 1980 (Bailey 1986). We obtained "sealing records" for marten pelts harvested across the entire Kenai Peninsula between 1988 and 2003 from the ADF&G. These records were identified by the minor drainage units in which marten were harvested and then plotted within the forested portions of each Uniform Coding Unit (UCU) in a Geographic Information Systems (GIS) (ArcMap 9.3). Together these records served to represent a rudimentary historic distribution of marten between 1905 and 2003.

Aerial Digital Videography Survey

Seven transects were flown at 150 m altitude over the KENWR to detect mammalian tracks in snow on 13 March 2006. Following a significant snowfall, weather conditions on the KENWR were cold, calm, and clear for 3 days preceding the survey, so that tracks were allowed to accumulate with minimal structural degradation. The ground was recorded with a Sony™ video camera linked to a GPS unit and laptop computer that recorded times and locations of each video frame into a Microsoft® Excel spreadsheet. Videotapes were later converted to a series of digital AVI video files using Adobe® Premiere Pro 2.0 software. Approximately 323,240 video frames were recorded at a rate of 30 frames per second, so that every fifth video frame (11.6 m wide) represented a unique image. Video files were analyzed on a frame-by-frame basis. Frames containing potential marten tracks were identified and saved as JPEG files during an initial analysis by a single technician. A set of 109 images containing potential marten tracks was reviewed a second time by the first technician and independently by a second technician familiar with furbearer tracks, and then a third time by the two technicians together in order to reconcile disputed frames. A subset of tracks identified as marten was also confirmed by a qualified wildlife biologist at the ADF&G. Frames containing marten tracks were cross-referenced with a flight log in order to assign times and locations to marten tracks and were then plotted in a GIS. We were not able to estimate detection rates through independent ground observations and were forced to assume equal detectability across all frames. Detections of marten therefore represent a presence-only dataset and likely underestimate the actual distribution of marten on the KENWR.

Carcass Necropsies

Ground-based field surveys composed of VHF telemetry in combination with back-tracking techniques were used to assess habitat, snow-cover, and resting site use at second and third order scales (Johnson 1980) in three study areas in the Kenai Mountains and Kenai Lowlands (Chapter 1). Interviews with area trappers, in concert with a KENWR program to

purchase carcasses, provided additional locations of marten harvested throughout the Kenai

Peninsula. We performed necropsies on carcasses and recorded sex, weight, body length, and

body fat measurements in order to identify differences in sex and age ratios, as well as body size

and condition among lowland and mountain populations. Potential differences in the overall

health of marten populations could demonstrate the effects of any variations in environmental

stress levels between regions. The third premolar was extracted to determine age of individuals

using cementum analysis, and corpora lutea were counted in ovaries to estimate the number of

reproductive females (Matson Laboratories, LLC, Milltown, MT). A series of four skull

measurements [greatest length (GTL), zygomatic breadth (ZB), length of the largest upper cheek

teeth (carnassial, PM4) and diameter of the upper canine (C)] were also measured using digital

calipers (Appendix A). Fat index, age and numbers of corpora lutea were analyzed using Chi-

square tests to evaluate the null hypothesis of no difference in carcasses sampled from the

lowlands versus those from the mountains (Proc FREQ, SAS Institute Inc. Cary, NC) whereas all

other measurements were compared among study areas using unpaired t-tests (Proc TTEST).

Climatological Monitoring

To characterize snow cover conditions within each study area, we established 19 snow

and temperature monitoring stations near roads and trails at predetermined elevations ranging

from 90 – 425 m (Figure 2.2). We placed two iButtons™ (Maxim Integrated Products, Inc.,

Sunnyvale, CA) at each station to record hourly air and subnivean temperatures near the ground.

We measured snow depths to the nearest cm with an avalanche probe at established stations each

day while working in a study area, and depths and densities at all stations at the beginning of each

month that snow was on the ground between February 2007 and May 2008. Average snow-pack

densities were measured by coring snow-packs with a 1.2-m-length of 5-cm-diameter PVC pipe

and weighing the contents with a spring scale to the nearest 5 g.

Using daily snow depth and minimum temperatures between 2000 and 2008 from 22 weather stations on the Kenai Peninsula, we calculated the average number of "stress-days" per month that occurred in the Kenai Lowlands, Kachemak Bay and Kenai Mountains regions, respectively. A stress day was defined as any 24-hour period during which snow cover (at a given density) was not deep enough to completely insulate the subnivean zone while temperatures fell below $-5°$ C (Marchand 1982). These calculations were used to tabulate the average number of days for which marten would need to seek out sites not associated with snow cover in order to limit thermodynamic costs while resting (Wilbert et al. 2000, Chapter 1). Stress days were tabulated given two theoretical snow densities of 0.1 and 0.2 g/ml. We used ANOVA to compare the average number of stress days per month (Oct-Apr) between 2000 and 2008 among regions and months, including a region*month interaction and accounting for differences in elevations at weather stations (Proc Mixed, SAS Institute Inc. 2005). We hypothesized that shallow early winter snow conditions common to the lowlands could expose marten there to more thermodynamically stressful conditions than those that typically occur at higher elevations in the mountains.

Trends in snowfall over time were determined from 25 Snotel and SnowCourse (McClure 2006) and 23 Western Regional Climate Center (WRCC) (Ashby 2008) weather stations on the Kenai Peninsula between 1931 and 2008. The station at Kasilof in the Kenai Lowlands began keeping records in 1931, 7 stations reported data for at least one year from 1950 – 1959, 12 stations between 1960 – 1969, 23 stations between 1970 – 1979, 35 stations between 1980 – 1989, 32 stations between 1990 – 1999, and 36 stations between 2000 – 2008. Yearly station maximums were stratified based on geographic clustering into three regions (Kenai Lowlands, Kachemak Bay, Kenai Mountains) to account for perceived geographic differences in weather patterns. We used a random coefficients model and included elevation as a covariate to compare linear trends in snow depth over time for each station and then averaged stations by region (Proc Mixed, SAS Institute Inc. 2005).

RESULTS

Historic Distribution

We found 28 independent records of marten occurring on the western Kenai Peninsula between 1905 and 1989 (Figure 2.3) (Bailey 1986, Magoun 1987, Schumacher et al. 1989, UC Berkeley Natural History Museum 2006). These included 7 specimens collected between 1905 and 1910 (UC Berkeley Natural History Museum 2006), 16 locations identified through trapper surveys (Bailey 1986, Magoun 1987, Schumacher et al. 1989) and 5 from annual KENWR trapping reports between 1950 and 1987. During 1910 – 1955, we could not find any records of marten occurring west of the Kenai Mountains. State of Alaska trapping regulations document that marten trapping was closed for at least 21 years on the western Kenai Peninsula between 1916 and 1960 because of perceived low population levels (Morton and Jozwiak 2008). In 1955, marten tracks were identified near Botenintin Lake, 30 km west of the mountains and at the time represented the westernmost detection of marten in 45 years. During 1960 – 1980, we identified 7 reports of marten in the western and southwestern Kenai Peninsula, some of which occurred as far west as the Swanson River watershed in 1980. Schumacher et al. (1989) identified tracks in the Kenai Mountain foothills, and they trapped and radio collared 11 individuals at Surprise Creek and Upper Russian Lake. At the time, these populations were believed to represent the westernmost extent of marten distribution on the peninsula.

Data from the ADF&G showed that since 1988, 1,103 marten pelts were sealed on the eastern side of the peninsula, compared to just 6 on the western side (Figure 2.3). Sealing records indicate the total harvest of between 3 and 146 marten from each UCU on the eastern peninsula and a total of just 6 marten from 4 UCUs on the western peninsula. All 4 units represent areas that were not included in previous distribution estimates of marten on the Kenai Peninsula.

Contemporary Distribution

We detected 32 independent occurrences of marten tracks on the KENWR during analyses of video track footage (Figure 2.4). Of these, 16 were located on 139.5 km (0.114 detections/km) of transect within a large post fire sere burned in 1947, one was located on 27.4 km of transect within the 1969 burn (0.036 detections/km), and 9 were located on 239.8 km (0.038 detections/km) of transect outside of burned areas (Figure 2.5). Four times as many marten per km surveyed were detected in the 1947 burn than in the 1969 burn, although the detection rate in the 1969 burn was roughly equal to that of unburned areas. Of the 32 tracks, 7 were located along 191.0 km (0.037 detections/km) of transects in beetle damaged forest, whereas 25 were along 345.7 km (0.072 detections/km) of transects in undamaged areas (Figure 2.6). This represents 2 times as many marten locations per km surveyed in undamaged forest.

In 2002, a single juvenile male marten was accidentally captured by KENWR staff near the Discovery Well hemlock stand in the Kenai Lowlands (Figure 2.2). A subsequent program initiated to purchase carcasses and information from area trappers yielded 90 locations of marten on the Kenai Peninsula since 2002, 53 of which occurred west of the Kenai Mountains (Figure 2.4). As part of the home-range component of this study, we captured 11 marten (4 at Upper Russian Lake, 1 at Surprise Creek in the Kenai Mountains, and 6 in the Kenai Lowlands) (Figure 2.4) (Chapter 1).

We collected and performed necropsies on 20 marten carcasses from the Kenai Lowlands and 39 carcasses from the Kenai Mountains. No significant differences were detected between the mountains and lowlands for body weight ($t_{57} = -0.33$, $P = 0.746$), body length ($t_{55.3} = -0.11$, $P = 0.911$), fat index ($X^2_3 = 5.30$, $P = 0.151$), age ($X^2_6 = 8.97$, $P = 0.175$), or any of the skull variables: greatest length ($t_{57} = 0.31$, $P = 0.757$), zygomatic breadth ($t_{56} = 0.22$, $P = 0.827$), upper carnassial length ($t_{57} = -0.82$, $P = 0.416$), or canine diameter ($t_{56} = -1.17$, $P = 0.248$) and so data were averaged across study areas (Table 2.1). We detected a difference between the number of

corpora lutea present in harvested females between the lowlands and mountains ($X^2_2 = 6.56$, $P =$ 0.038). Of 9 adult females collected from the lowlands 67% showed evidence of past pregnancies in contrast to just 1 in the mountains ($n = 8$) (Appendix A).

Snow and Temperature

Subnivean temperatures at project snow stations were directly related to snow cover. Stations with snow depths less than about 30 cm during cold spells showed subnivean temperature depression below –3ºC, exemplified by the Discovery Well hemlock stand station (90 m elevation) in the western Kenai Lowlands between 12 January 2007 and 31 March 2007 (Figure 2.7). In contrast, snow depths in the mountains, at the Surprise Creek (450 m) station, for example, remained well above the hiemal threshold and consequently, subnivean temperatures did not fall below –4º C over the course of the 2007 winter despite ambient temperatures reaching as low as –23º C between 2 February 2007 and 1 April 2007 (Figure 2.8). Overall snow densities increased during the winter and were, on average, lower in the lowlands ($\bar{x} = 0.214$ g/cm^3, SE = 0.007) than in the mountains ($\bar{x} = 0.286$ g/cm^3, SE = 0.012) ($F_{16} = 21.66$, $P < 0.001$) (Figure 2.9) between January 2007 and May 2008.

At an approximate early season snow density of freshly fallen snow (0.1 g/cm^3) we found that the average number of stress days was inversely related to elevation, decreasing by 0.178 days for every 100-m increase in elevation ($F_{1,132} = 19.98$, $P < 0.001$). The number of stress days also differed by month ($F_{6,132} = 8.68$, $P < 0.001$). November was by far the most stressful month, averaging 9.0 days per year (SE = 1.123), nearly twice as many as the next most stressful month of December ($\bar{x} = 4.6$; SE = 1.102) (Figure 2.10). Stress days did not differ among regions when elevation was accounted for ($F_{2,132} = 1.88$, $P = 0.157$) (Figure 2.11).

At a more realistic accumulated snow density of 0.2 g/cm^3, differences were more evident. The average number of stress days decreased by 0.202 days for every 100-m increase in

elevation ($F_{1,132} = 17.06$, $P < 0.001$). The number of stress days also differed by month ($F_{6,132} = 13.51$, $P < 0.001$). Again, November was by far the most stressful month, averaging 13.2 days per year (SE = 1.412), followed by December ($\bar{x} = 8.8$, SE = 1.172) and January ($\bar{x} = 6.4$, SE = 1.486) (Figure 2.10). At a theoretical snow density of 0.2 g/cm^3, stress days did not differ among regions when elevation was accounted for ($F_{2,132} = 0.10$, $P = 0.909$) (Figure 2.12).

Linear regressions indicated that average maximum snow depths were directly related to elevation ($F_{1,44} = 10.38$, $P = 0.001$) and when elevation was accounted for, regressions indicated that snow depths have increased between 1931 and 2008 ($F_{1,47} = 4.81$, $P = 0.033$). Depths in the Kenai Mountains have been increasing by 0.29 cm/year since 1951 ($t_{45} = 2.12$, $P = 0.040$). Slopes of 0.17 cm/year in the Kenai Lowlands since 1931 ($t_{45} = 0.93$, $P = 0.355$), and 0.08 cm/year in the Kachemak Bay region since 1952 ($t_{45} = 0.32$, $P = 0.749$) were not significant (Figure 2.13).

DISCUSSION

Comparisons between the historic and contemporary locations of marten suggest that marten may have expanded their distribution westward across the Kenai Peninsula over the past 50 years. The absence of occurrences between 1910 and 1955 indicate that marten could have disappeared from the western Kenai Peninsula during that time. This may have been the result of the strychnine poisoning program targeted at wolves (*Canis lupus*) between 1898 and 1915, but which also affected many other furbearers including marten (Palmer 1938). Baughman (1917) reported a resurgence of mink (*Mustela vison*), red fox (*Vulpes vulpes*), and lynx (*Lynx canadensis*) following the cessation of poisoning efforts on the Kenai Peninsula, however there is no direct evidence showing the effects on marten. Beginning with the location at Botenintin Lake in 1955, reports of marten on the western Kenai became increasingly common. Conclusions based on historic records and anecdotal observations can, however, be spurious as a result of

biases in sampling effort. However, because of the repeated and consistent documentation of an absence of marten during the mid-20th century, followed by their subsequent identification in the lowlands, we believe our data provide evidence of the re-colonization of marten on the western peninsula following extirpation around the turn of the 20th century.

The explanation for their recent re-emergence may be related to a combination of several landscape-level phenomena driven by climate change. We suspect that the Kenai Lowlands generally represents an area of suboptimal habitat, given its shallow snow cover, cold temperatures, active fire history, and younger stand age, especially in comparison to mountainous areas containing higher marten densities. Snow densities measured in the lowlands during 2007 and 2008 would have required the accumulation of at least 26 cm to 49 cm of snow in order to meet the hiemal threshold. Because these conditions are often not met, marten in the lowlands appear to have adapted by seeking out alternative resting sites such as squirrel middens which provide them with warm, dry resting sites comparable in insulation to resting sites under the snow (Buskirk 1984, Chapter 1). Their ability to adapt behaviorally to the more stressful thermodynamic conditions at lower elevations may have allowed marten to overcome many of the environmental constraints of the lowlands.

Conditions such as the cold temperatures and shallow snow-packs common to the lowlands, perhaps do not pose a major obstacle for marten inhabiting the mountains where the hiemal threshold is more easily surpassed. Snow densities in the mountains are often greater than in the lowlands, but because depths normally exceed 50 cm, snow cover there is more than sufficient to keep the subnivean zone insulated throughout the winter (Marchand 1987). Stress-day calculations highlight this important difference in available snow-packs and how it can translate into potentially elevated levels of thermodynamic stress for marten and their prey at lower elevations. The majority of stress days occurred between November and January, indicating that marten are exposed to suboptimal conditions primarily during the late fall and early winter before the hiemal threshold has been met.

The insulating effects of snow are also crucial for the survival of subnivean-dwelling prey, which depend on sufficient snow-cover to insulate them from cold ambient temperatures in winter. Deep snow prevents the soil from freezing which translates into higher thermal efficiency for subnivean-dwelling small-mammals (Formozov 1965, Marchand 1983, 1987). While deep snow often hinders foraging for many predators (raptors, lynx, red fox), the ability of marten and weasels (*Mustela spp.*) to access the subnivean zone allows them to exploit this untapped prey base (Formozov 1965).

Although we did not examine prey availability in this research, some evidence suggests that populations of voles (Subfamily: *Arvicolinae spp.*) have higher survival rates during winter in years of deep snow cover (Formozov 1965, Mellander et al. 2005, Boonstra and Krebs 2006, Solonen 2006) and may ultimately be an indicator of the quality of an area for marten (Merritt et al. 2001, Solonen 2006, Boonstra and Krebs 2006). Additionally, Solonen (2006) reported a decline in winter survival of small mammals and a decrease in spring densities as a result of winter temperatures that "sea-sawed" across the freezing point. Small mammal trapping success and species diversity were also reported to increase with a rise in elevation on the Kenai Peninsula, potentially the result of differences in habitat quality, quantity (Fuller 1981) or deeper snow.

Despite their use of squirrel middens as resting sites in the Lowlands, harvest and live-capture rates indicate that conditions on the Kenai Lowlands may not be conducive to supporting marten populations as dense as those in the mountains. Capture rates of marten in the lowlands were 1.2 % compared to 3.1 % in the mountains (Chapter 1). Additionally, ADF&G sealing records indicate the harvest of 92 times more marten in the mountains than in the lowlands, and average annual harvests in the mountains have increased four-fold since 1989 (Morton and Jozwiak 2008). This may indicate a burgeoning marten population in the mountains, capable of expanding into largely unoccupied habitat in the lowlands. The extent to which marten populations on the lowlands will be successful, however, remains to be seen.

One might expect that suboptimal ambient conditions and the potential for increased thermal stress at lower elevations might result in poorer population health there. We found body weights and fat reserves of necropsied marten from the lowlands to be marginally, but not significantly lower than those from mountain populations (Table 2.1, Appendix A). The large percentage of gravid females in the lowlands also indicates the presence of an established, breeding population there (Appendix A). These data support the notion that marten at low elevations are in fact largely compensating for their more stressful environment by utilizing alternative resting sites and are finding sufficient prey to satisfy thermodynamic requirements.

Although spruce forests that have been killed by spruce-bark beetles contain an abundance of CWD, these areas do not appear to represent quality habitat for marten. While the high density of CWD and snags may initially provide protection, resting sites, and prey for marten (Chapin et al. 1997, 1998, Bull et al. 2005), their open canopies likely detract from their suitability as marten habitat by exposing them to predation, especially reproductive females protecting kits (Paragi et al. 1996). Our data, which suggest a tendency of avoiding beetle-killed forests, would support this assertion. Furthermore, in the Surprise Creek study area, where bark beetles have killed the majority of mature white/Lutz spruce over the past 10 – 15 years, surveys in 2007 documented just one marten (Chapter 1). This is in marked contrast to the 5 marten identified there during 1986 – 1988 (Schumacher et al. 1989).

Over the long term, following extensive white spruce beetle-kill and blow-down, *Calamagrostis spp*. grasses frequently emerge as the dominant ground cover, excluding shrub succession and spruce cone establishment for as long as 100 years (Matsuoka et al. 2001, Boggs et al. 2008). A grass-dominated understory devoid of berry-producing shrubs and mycorrhizal fungi will likely not provide red-backed voles with adequate forage (Maser et al. 1978). Red-backed voles, the primary prey of marten, increase in response to greater understory cover but have been shown to decrease in areas after clear-cutting and beetle infestation (Maser et al. 1978, Nordyke and Buskirk 1991, McDonough and Rexstad 2005). Red squirrel densities have also

been shown to decrease in response to beetle infestations, likely stemming from a reduction in the number of mature, cone-producing trees (Koprowski et al. 2005). The absence of these species would ultimately result in an insufficient prey base for marten.

Post-fire seres are similar to beetle-killed forests, in that while they may initially contain sufficient levels of CWD, their complete lack of over-story canopy cover, and consequent increase in predation risk, may preclude marten from permanently inhabiting such areas until significant regeneration has occurred (Koehler and Hornocker 1977, Paragi et al. 1996). We believe the time required to allow burned forests to regenerate into mature coniferous forests could explain the disparity in marten detections in the 1947 and 1969 burns. However, the small sample size in the 1969 burn and the nearly equal detection rates of marten there and in unburned areas make it difficult to form solid conclusions. After 59 years, the area burned by the 1947 fire has regenerated into a mature coniferous forest, with ample cover and structure suitable for supporting marten and their prey. In contrast, after 37 years, most of the area burned by the 1969 fire is dominated by northern hardwood species and immature coniferous saplings, which do not provide sufficient cover or structure for marten. The burning of such a large proportion of the lowlands in 1947 could partially explain the absence of marten there during the latter half of the 20th century, however marten were also not detected in those areas for 37 years before the 1947 fire occurred. Younger post-fire seres also lack the underbrush necessary to support large prey populations. Without sufficient structure and canopy closure, these areas may decline in their importance to marten. As climate change alters the fire regime on the Kenai, the land area available as suitable marten habitat could decline.

Although marten distribution on the Kenai Peninsula appears to have expanded over the past 100 years, is this a trend that can be expected to continue in the context of a warming climate? A recent study that compared the skulls of 400 marten collected in Alaska determined that the average skull lengths of marten have increased by 0.03% over the past 50 years (Yom-Tov et al. 2008). Data collected from carcass collections indicate that marten on the Kenai are

similar in size, if not marginally larger than those measured by Yom-Tov et al. (2008) (Appendix A). The increase in body size is attributed to shorter, warmer winters that have allowed for increased plant growth and a resultant increase in the size and availability of voles and shrews (Subfamily: Soricinae *spp*.) (Yom-Tov and Yom-Tov 2005, Yom-Tov et al. 2008). All other environmental factors aside, an increase in small mammal body sizes would benefit marten by increasing caloric intake and could aid in their continued expansion (Yom-Tov et al. 2008).

Marten populations thrive in mature forests, with closed canopies, complex structure, and a consistent, deep snow-pack. The interplay of several forces related to climate change will certainly alter all three of these habitat components and ultimately shape the future of marten on the Kenai Peninsula and throughout their range. Warmer temperatures will likely reduce thermal stress exerted on marten especially in the lowlands. The importance of snow cover as a resting site component may be marginal given the continued availability of squirrel midden resting sites, regardless of whether current snow depth trends hold as temperatures warm. As the Kenai continues to dry and the fire regime shifts over the coming decades, lowland spruce forests may be converted to early successional hardwood stands and grassland less suitable for marten. More frequent spruce-bark beetle outbreaks could increase the amount of woody-debris available as potential resting sites, but would at the same time decrease over-head cover and the prey base. This habitat loss may be partially offset by the comparatively slow upward expansion of closed-canopied forests into areas of alpine tundra already maintaining sufficient snow-packs. Warmer temperatures may cause a redistribution of marten across the Kenai as they continue to seek thermally efficient resting sites in light of changing snow, habitat, and prey conditions.

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Table 2.1. Marten carcass and skull measurements for 59 marten harvested on the Kenai Peninsula, Alaska, USA between 2006 and 2008.

Variable	n	$\bar{x}$	SE
length[a]	59	59.66	0.58
weight [b]	59	807.03	24.63
fat index	59	1.73	0.13
GTL[c]	59	84.49	0.63
ZB[d]	59	46.45	0.84
PM4[e]	59	7.66	0.07
C[f]	58	4.07	0.05

[a] Body length measured from end of nose to tip of tail
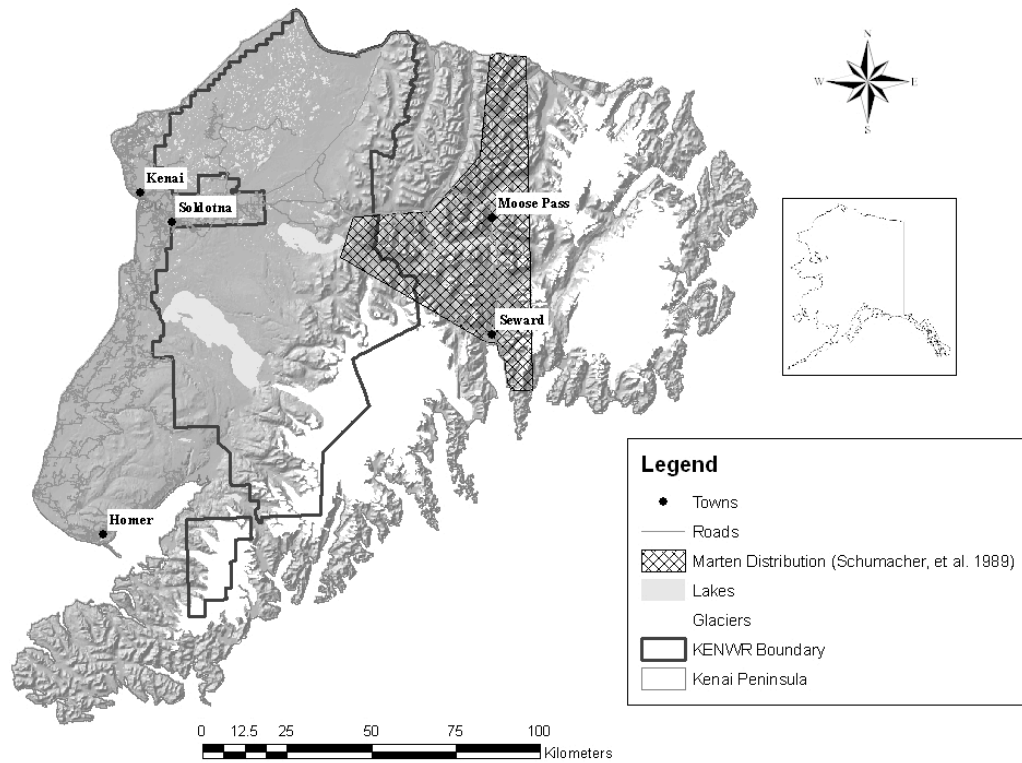[b] Body weight did not include pelts
[c] Greatest length of skull
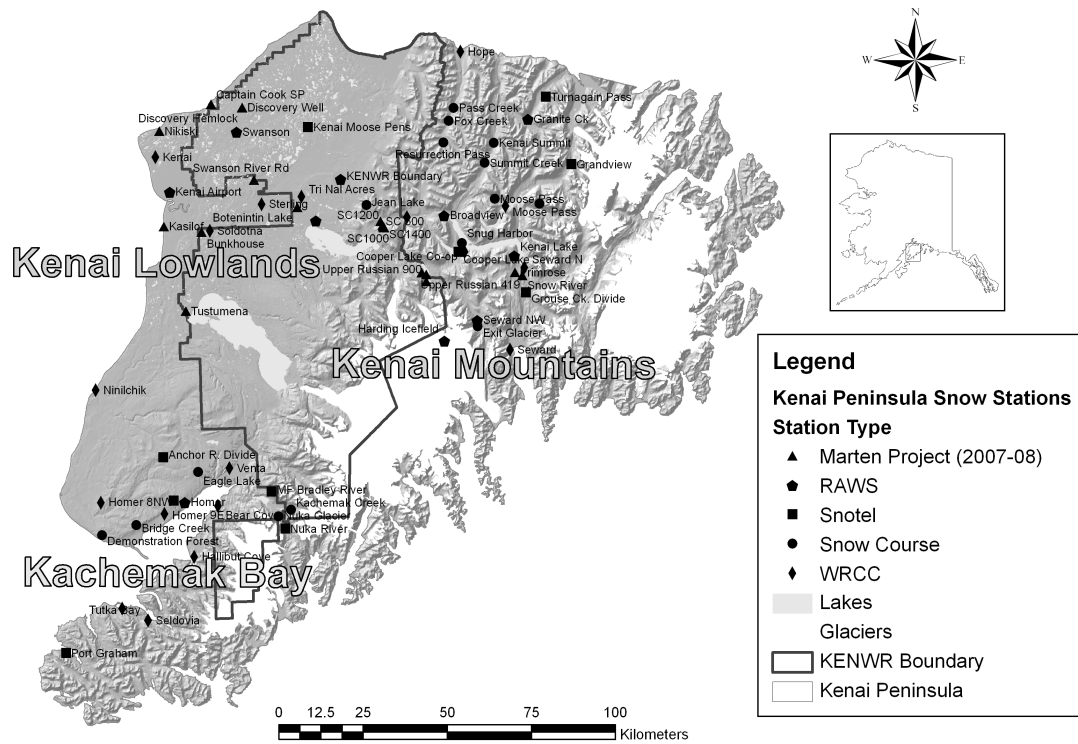[d] Greatest zygomatic breadth
[e] Greatest length of fourth upper premolar
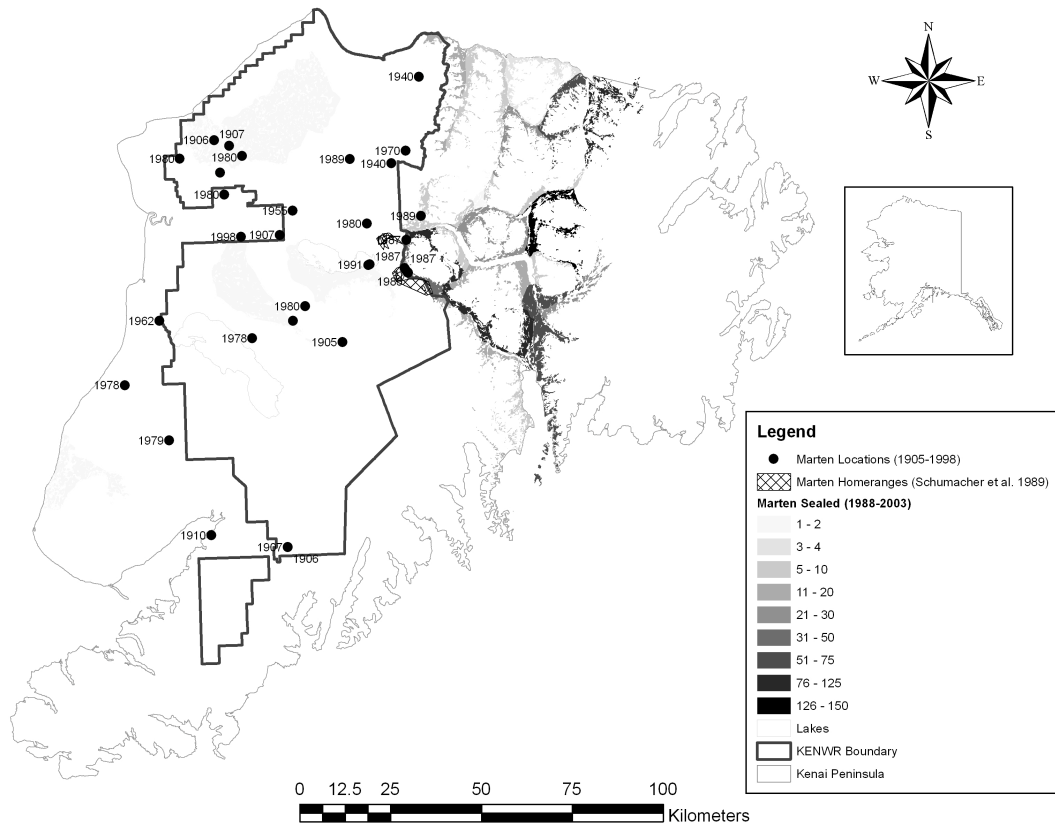[f] Greatest width of upper canine

Figure 2.1. Estimated distribution of American marten on the Kenai Peninsula, Alaska, USA as of 1989 (Schumacher et al.) in relation to Kenai Peninsula towns and geographic regions.

Figure 2.2. Locations of all weather stations that supplied snow depth and temperature for climatological analyses on the Kenai Peninsula, Alaska.

Figure 2.3. Historical locations of American marten on the Kenai Peninsula, Alaska, USA between 1905 and 2003, collected from trapper surveys, U.S. Fish and Wildlife reports, Alaska Department of Fish and Game reports, and a Kenai National Wildlife Refuge study (Schumacher et al. 1989).
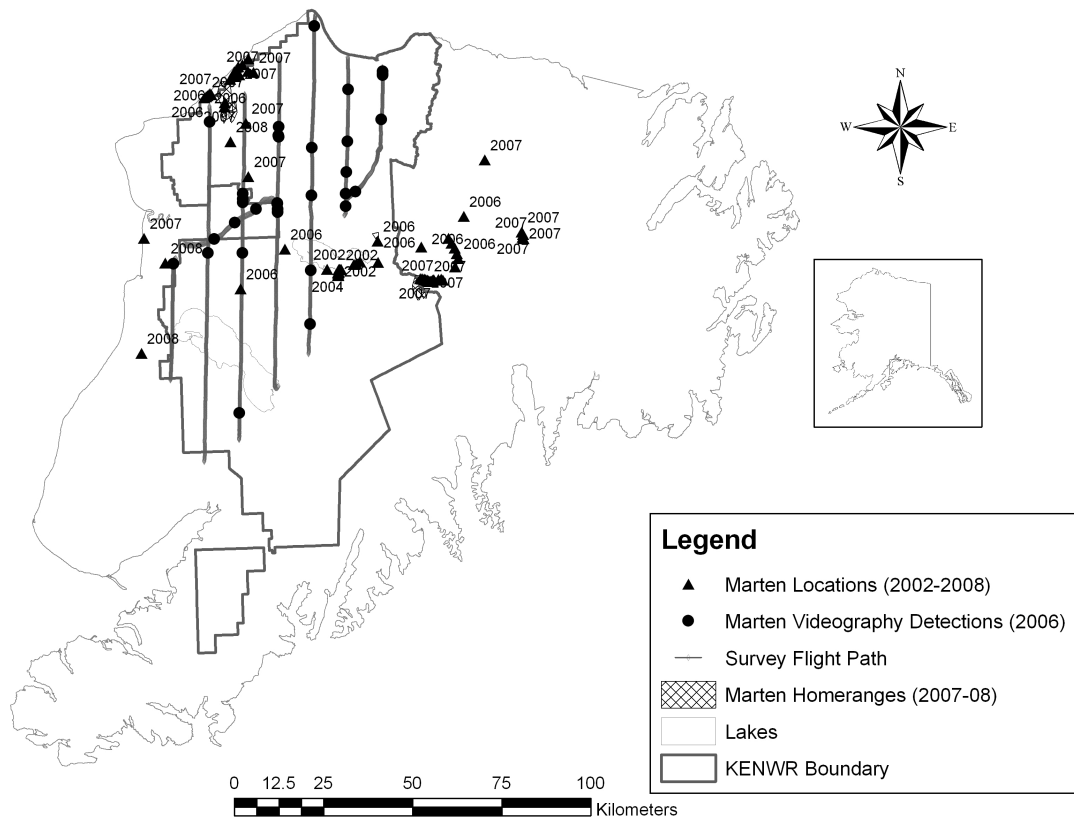
Figure 2.4. Contemporary, presence-only locations of American marten on the Kenai Peninsula, Alaska, USA between 2002 and 2008 using aerial digital videography, trapper surveys, and a home-range study (Chapter 1).
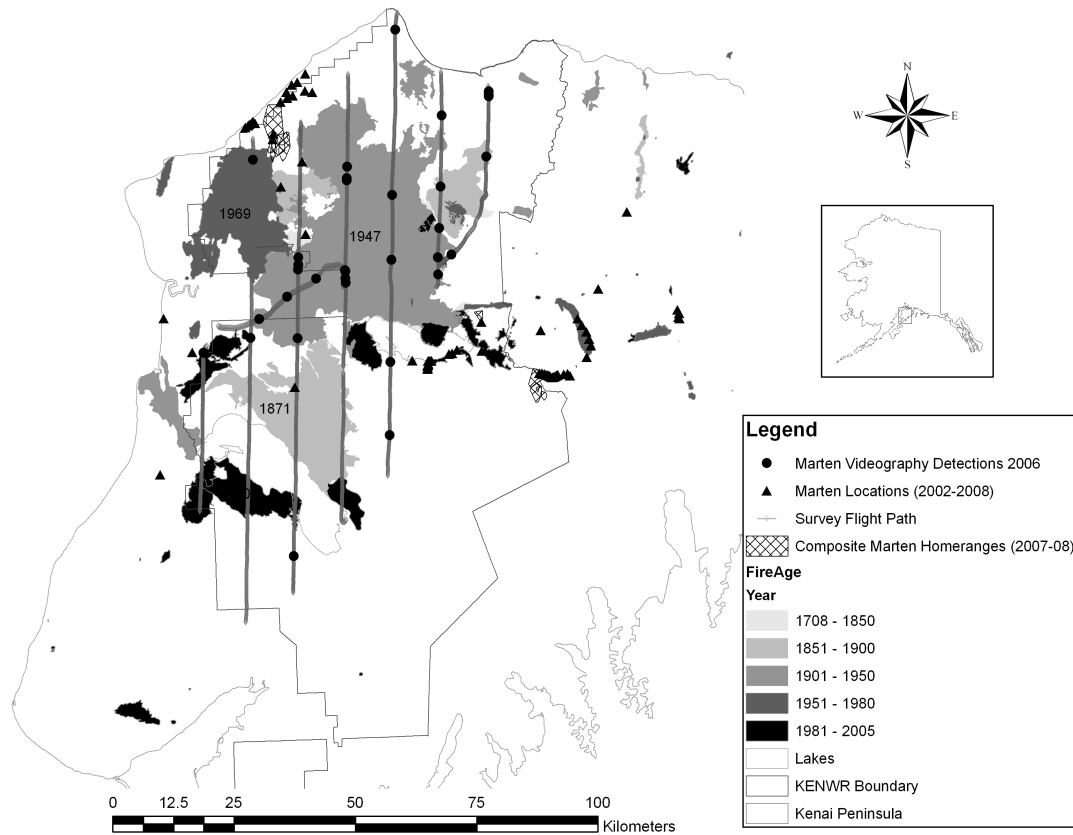
Figure 2.5. Contemporary, presence-only detections of American marten using aerial digital videography, trapper surveys, and a home-range study (Chapter 1) between 2002 and 2008 in relation to fire history, specifically the 1947 and 1969 burns on the Kenai Peninsula, Alaska, USA.
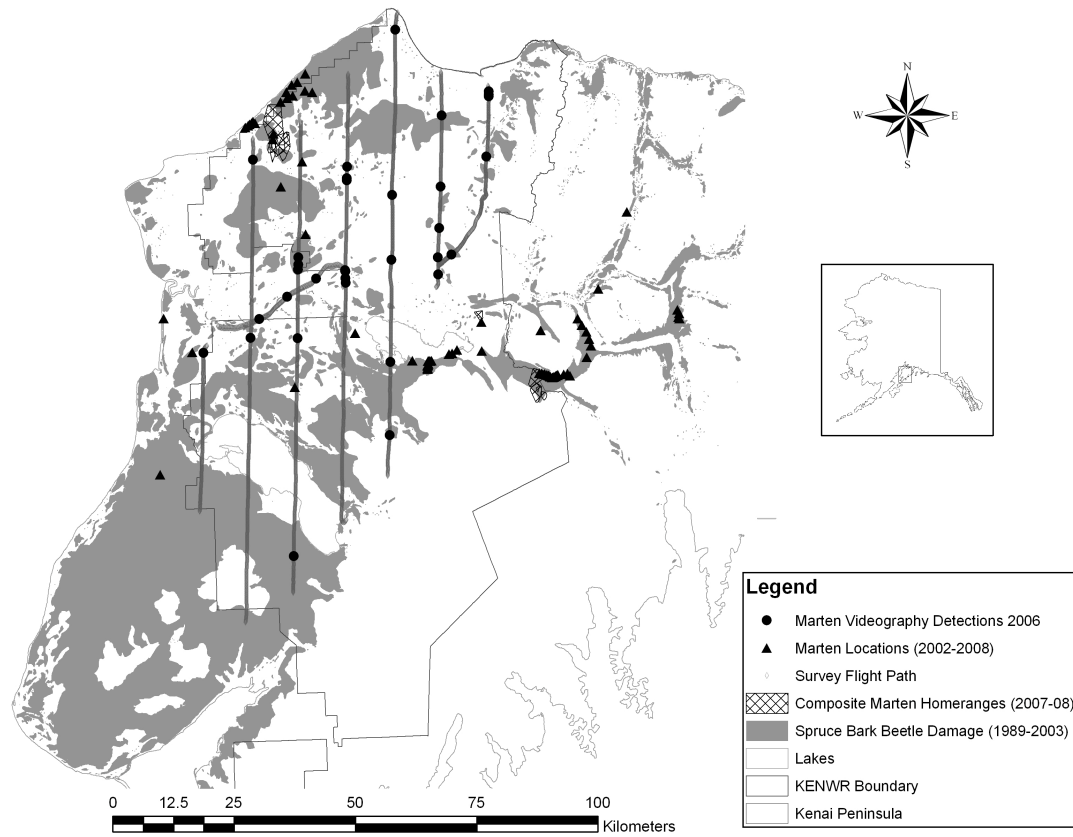
Figure 2.6. Contemporary, presence-only detections of American marten using aerial digital videography, trapper surveys, and a home-range study (Chapter 1) between 2002 and 2008 in relation to spruce bark beetle damage on the Kenai Peninsula, Alaska, USA.
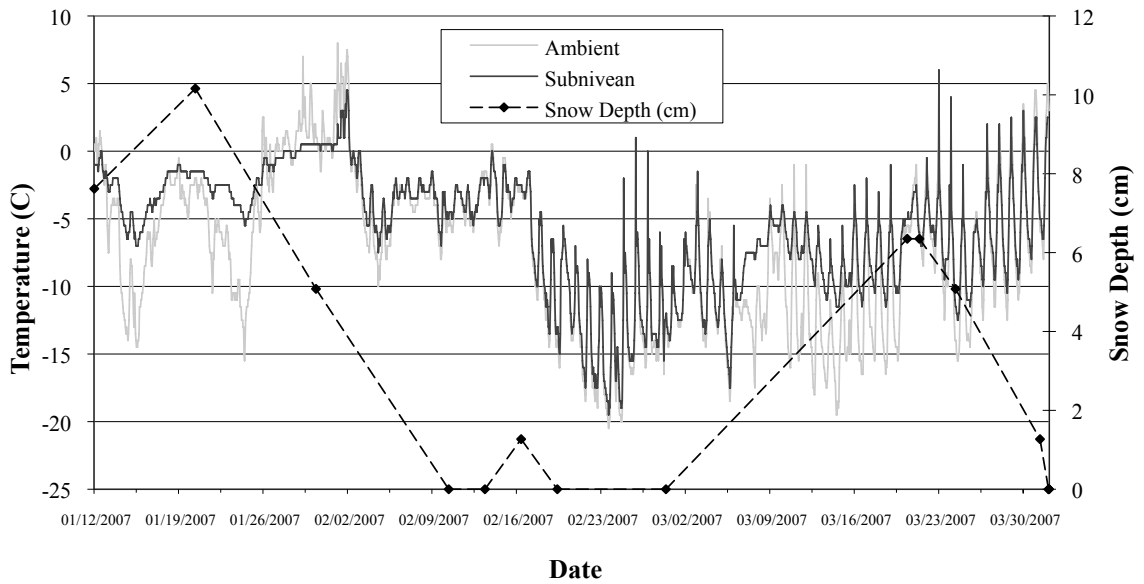
Figure 2.7. Subnivean and ambient temperatures measured every hour in relation to snow depth at a weather station in a dense canopy hemlock stand at 90 m elevation in the Kenai Lowlands on the Kenai Peninsula, Alaska, USA during Winter 2007.
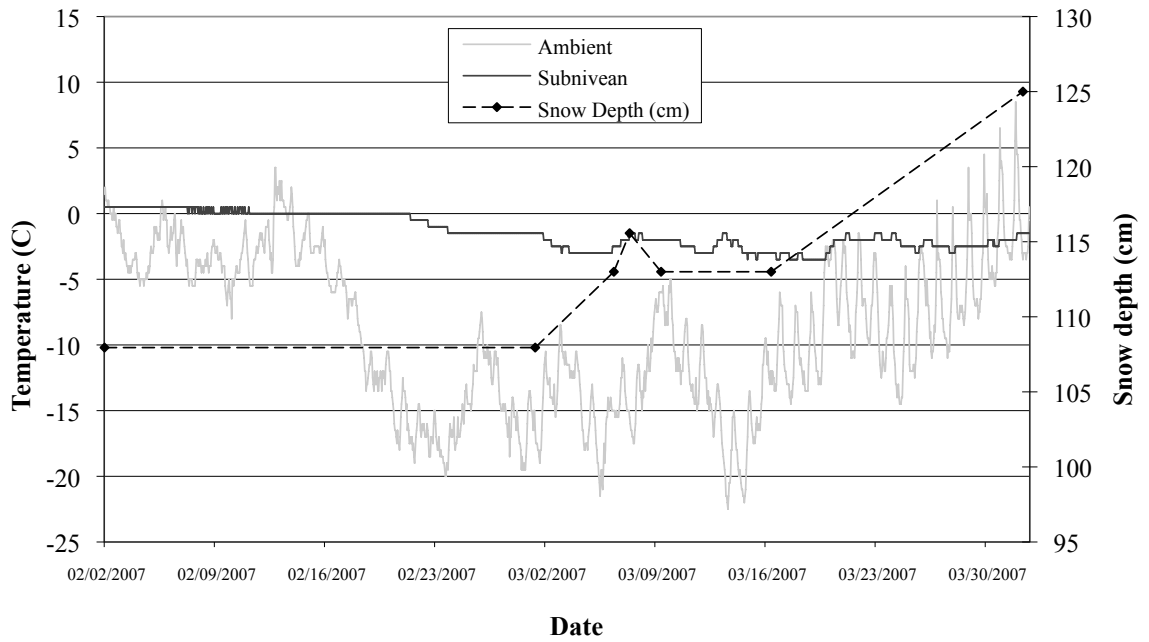
Figure 2.8. Subnivean and ambient temperatures measured every hour in relation to snow depth at a weather station in an open white spruce/hemlock stand near treeline at 450 m elevation at Surprise Creek in the Kenai Mountains on the Kenai Peninsula, Alaska, USA during Winter 2007.
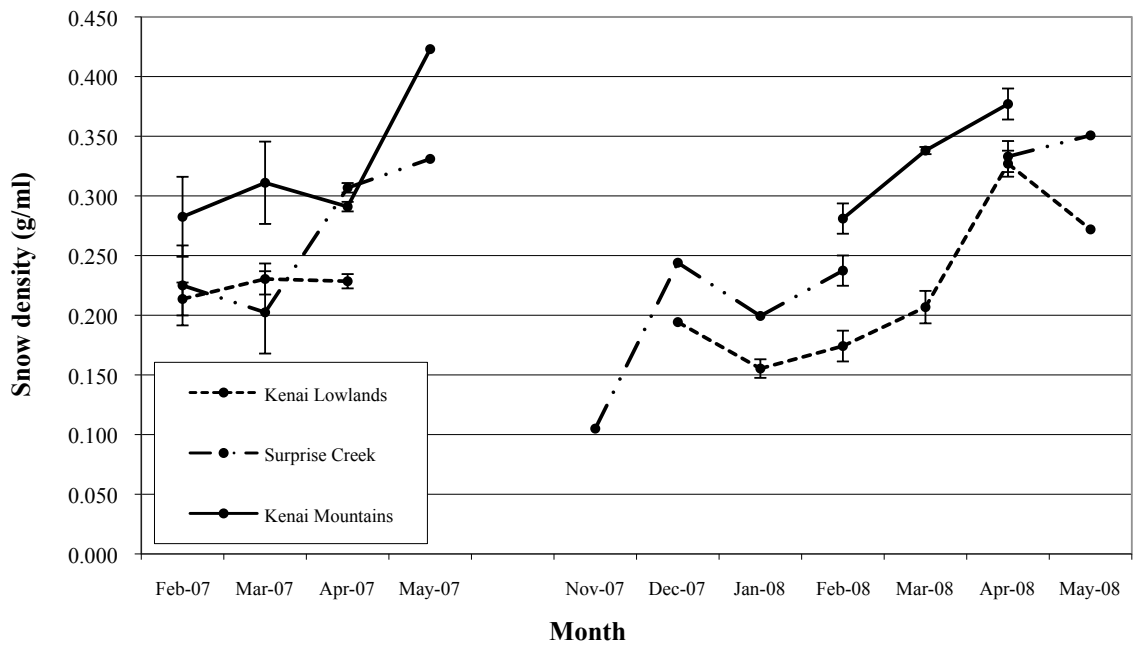
Figure 2.9. Average snow densities at weather stations in the Kenai Lowlands and Kenai Mountains on the Kenai Peninsula, Alaska, USA during the winters of 2007 and 2007-08.
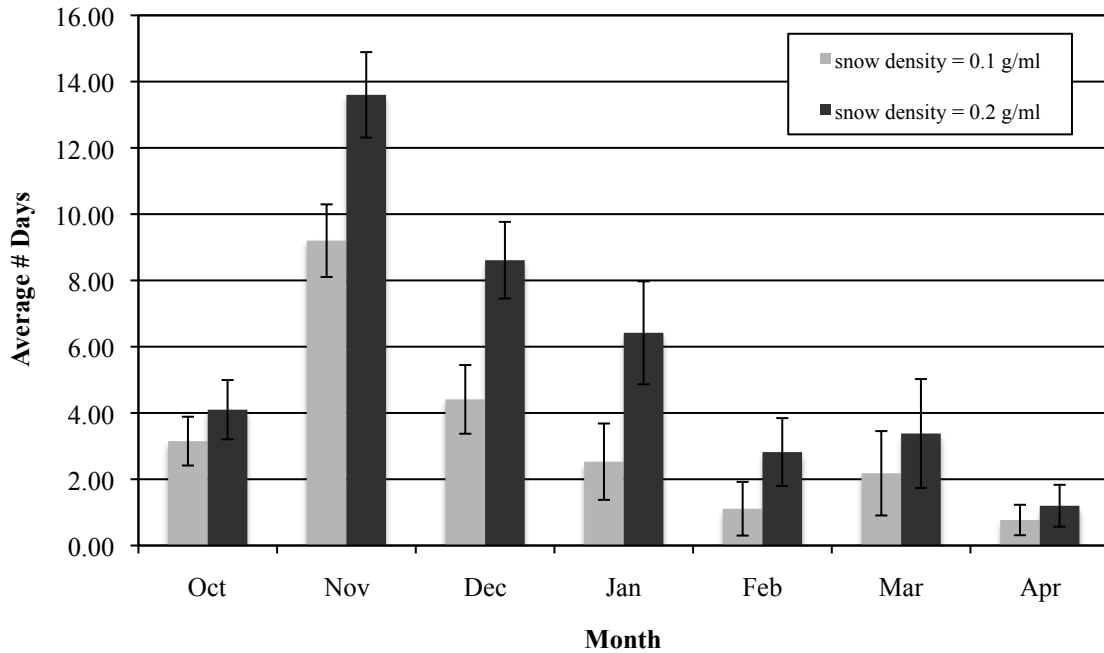
Figure 2.10. Average number of stress-days (days during which snow-packs did not meet the hiemal threshold (depth <20 cm, density = 0.1 g/ml; depth <40 cm, density = 0.2 g/ml) pooled across 22 weather stations on the Kenai Peninsula, Alaska, USA between 2000 and 2008.
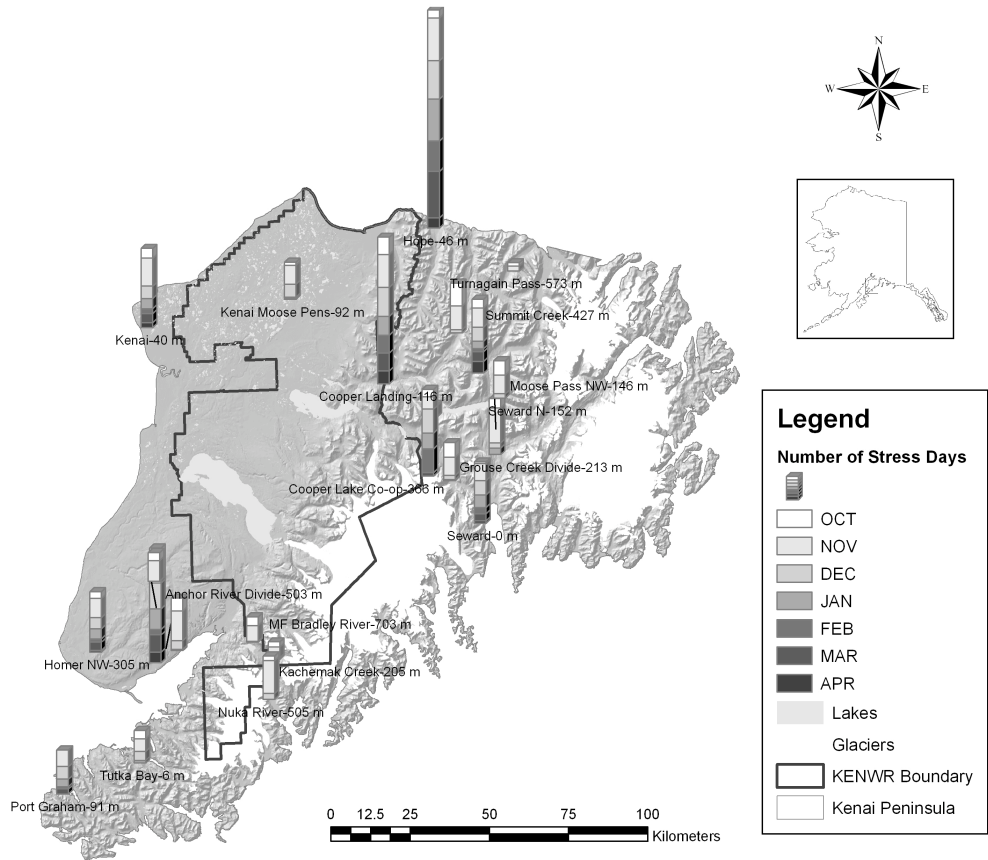
Figure 2.11. Geographic distribution of the average number of stress days (days during which snow-packs did not meet the hiemal threshold (depth <20 cm, density = 0.1 g/ml) during winter months at 22 weather stations on the Kenai Peninsula, Alaska, USA between 2000 and 2008.
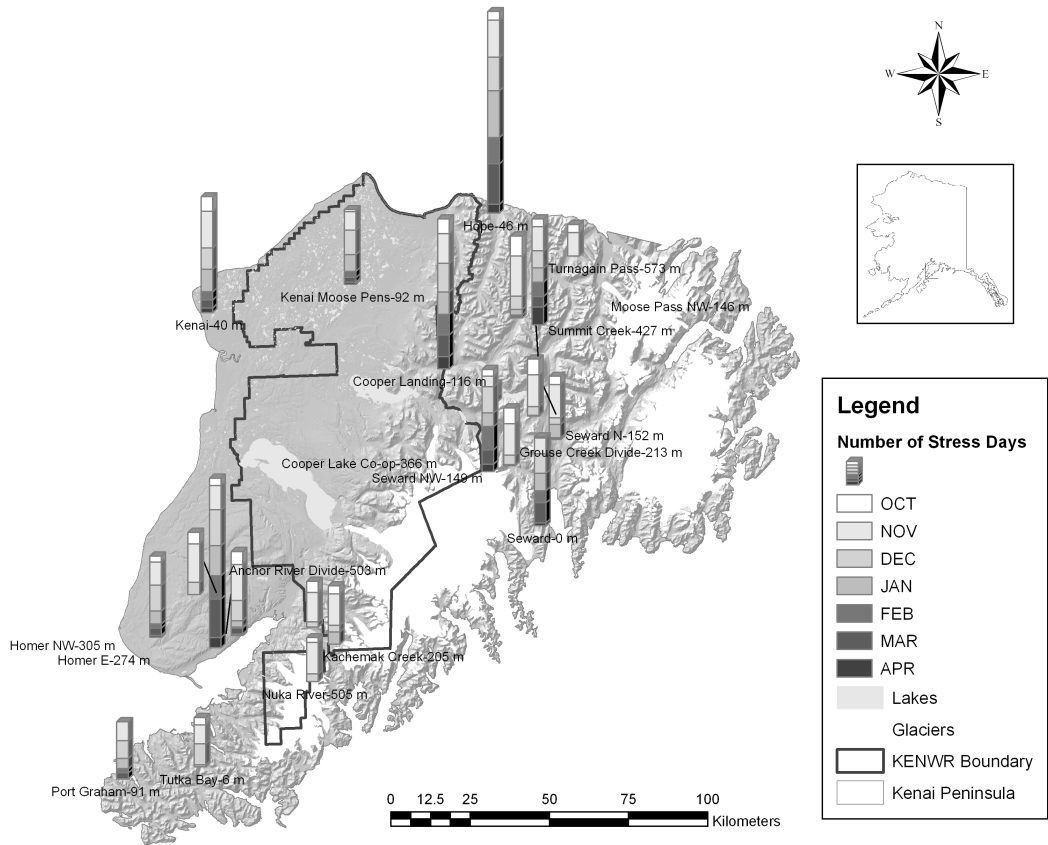
Figure 2.12. Geographic distribution of the average number of stress days (days during which snow-packs did not meet the hiemal threshold (depth <40 cm, density = 0.2 g/ml) during winter months at 22 weather stations on the Kenai Peninsula, Alaska, USA between 2000 and 2008.
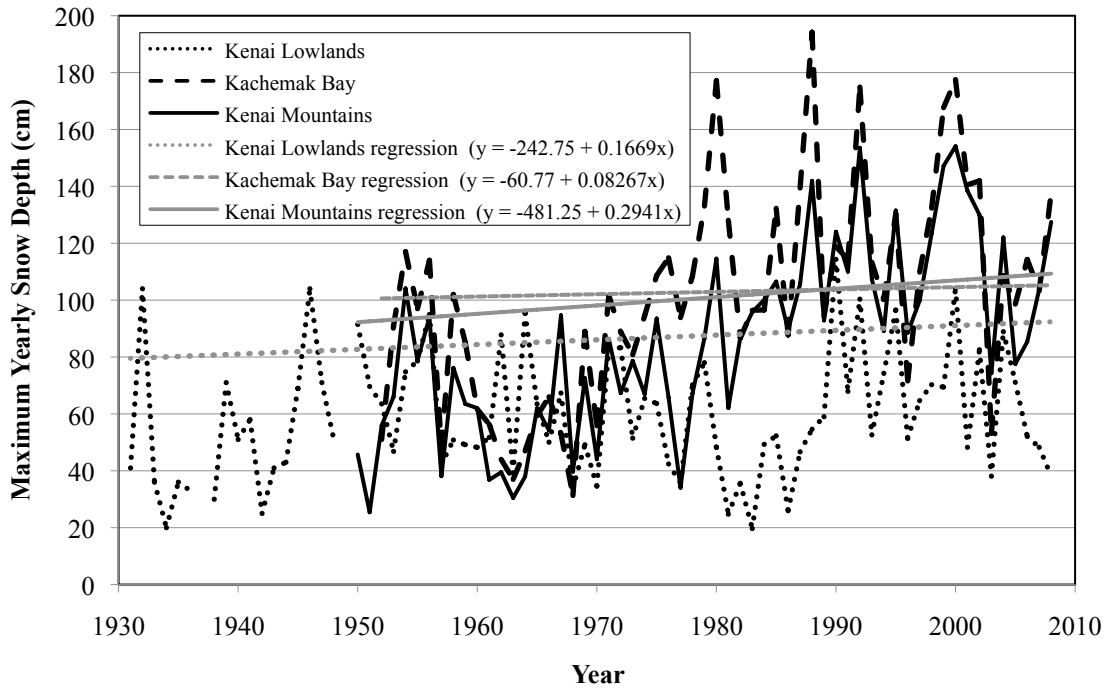
Figure 2.13. Maximum yearly snow depths, linear regression lines, and regression equations adjusted by elevation for 48 meteorological stations in 3 regions on the Kenai Peninsula, Alaska, USA between 1931 and 2008.

Appendix A. Necropsy results for marten carcasses collected from trappers on the Kenai Peninsula, Alaska between 2006 and 2008.

ID#	Study area	Sex	Body Length[a] (cm)	Body weight[b]	Fat Index	GTL[c] (mm)	ZB[d] (mm)	PM4[e] (mm)	C[f] (mm)	Age	Corpora lutea
M06-01	Mountain	M	58.5	900	2	87.09	45.54	8.23	4.34	0	
M06-02	Mountain	M	59.0	830	1	88.60	49.51	8.41	4.60	2	
M06-03	Lowland	F	56.5	670	1	80.26	42.77	7.35	3.93	2	3
M06-04	Lowland	F	57.0	610	1	79.02	43.22	6.71	3.51	2	3
M06-05	Lowland	F	56.0	590	2	79.76	41.36	6.71	3.42	1	0
M06-06	Lowland	M	65.0	790	1	90.15	45.83	7.23	4.09	0	
M06-07	Lowland	M	62.0	880	2	89.07	49.30	7.28	4.49	2	
M06-08	Lowland	M	65.0	1110	3	90.50	51.18	8.30	4.29	5	
M06-09	Mountain	F	56.0	620	4	80.81	42.38	7.38	3.82	0	0
M06-10	Mountain	F	54.5	600	2	78.34	40.29	7.56	3.65	0	0
M06-11	Mountain	F	80.5	540	1	79.21	42.23	7.62	3.81	0	0
M06-12	Mountain	F	54.0	505	1	78.36	40.46	7.35	3.70	0	0
M06-13	Mountain	M	62.0	810	1	88.46	50.49	7.96	4.46	2	
M07-01	Lowland	M	61.0	940	2	87.46	50.50	8.48	4.47	4	
M07-02	Lowland	F	58.0	590	1	81.30	43.86	8.25	3.68	1	3
M07-03	Lowland	M	61.5	1050	1	89.42	49.37	7.74	4.32	3	
M07-04	Lowland	F	55.0	685	1	78.51	43.64	7.02	3.62	3	0
M07-05	Lowland	M	60.0	1050	2	89.72	49.81	7.70	4.05	3	
M07-06	Lowland	F	57.0	710	2	79.27	43.35	8.11	3.75	1	0
M07-07	Lowland	F	59.5	780	2	83.10	44.22	8.30	3.82	8	3
M07-08	Lowland	M	61.5	850	2	87.69	86.86	7.87	4.25	1	
M07-09	Lowland	M	64.5	1005	1	91.93	48.95	8.27	4.63	2	
M07-10	Mountain	M	65.5	1000	1	90.45	48.93	7.66	4.31	2	
M07-11	Mountain	M	61.5	910	4	85.76	44.38	7.73	4.24	0	
M07-12	Mountain	F	56.0	645	2	79.40	41.85	7.57	3.84	1	0
M07-13	Mountain	F	55.5	810	4	79.21	42.35	7.15	3.76	0	0
M07-14	Mountain	M	62.5	1100	4	89.09	52.08	7.92	4.24	3	
M07-15	Mountain	M	64.0	1060	1	91.71	52.03	8.44	4.63	2	
M07-16	Mountain	M	63.0	1190	4	90.93	51.51	7.79	4.35	2	
M07-17	Lowland	M	58.0	910	1	88.53	45.94	8.01	4.34	0	
M07-18	Lowland	F	57.0	680	1	79.89	43.41	6.72	3.59	5	3
M07-19	Lowland	M	62.0	850	2	88.57	49.51	8.11	4.26	1	
M07-20	Lowland	F	58.0	650	1	79.87	42.14	7.22	3.75	2	4
M07-21	Mountain	F	57.5	650	2	81.37	42.48	7.01	3.85	1	0
M07-22	Mountain	F	58.0	760	3	81.81	43.40	7.43	3.78	2	4
M07-23	Mountain	M	61.0	900	1	88.03	47.05	7.69	4.45	2	
M07-24	Mountain	M	60.5	995	3	86.86	49.66	8.10	4.46	2	
M07-25	Mountain	M	64.0	965	3	88.90	49.28	8.37	4.14	1	
M08-01	Lowland	F	57.2	515	1	81.31	43.81	6.30	3.63	2	
M08-02	Mountain	M	55.9	610	1	79.87	42.12	7.28	3.96	0	

M08-03	Mountain	M	59.7	880	2	88.94	50.98	8.37	4.64	7	
M08-04	Mountain	M	61.0	880	1	89.79	50.09	8.03	4.40	3	
M08-05	Mountain	F	54.6	600	1	80.37	43.93	7.26	3.85	6	
M08-06	Mountain	M	59.1	860	1	85.41	44.71	7.80	4.55	0	
M08-07	Mountain	F	50.8	340	1	77.57	41.15	7.10		0	
M08-10	Mountain	M	66.7	1010	2	90.94	45.63	8.33	4.31	0	
M08-11	Mountain	M	58.4	860	1	86.44	44.92	8.04	3.84	0	
M08-12	Mountain	M	62.2	880	1	85.90	44.78	8.10	4.03	0	
M08-13	Mountain	M	64.8	1170	3	90.43	51.50	8.07	4.56	9	
M08-14	Mountain	F	53.3	660	1	77.04	41.16	7.22	3.79	0	
M08-15	Mountain	F	57.2	610	1	80.21	43.64	7.36	3.89	6	
M08-16	Mountain	F	57.2	690	2	80.24	43.96	6.97	3.77	2	
M08-17	Mountain	M			1						
M08-18	Mountain	M			1						
M08-19	Mountain	F	56.5	620	1	78.75	40.93	7.16	3.53	0	
M08-20	Mountain	F	55.2	790	3	77.74	42.18	7.17	3.58	0	
M08-21	Mountain	M	64.8	1030	1	89.55	50.95	8.37	4.35	2	
M08-22	Mountain	F	55.9	640	1	78.78	41.41	6.86	3.73	1	
M08-23	Mountain	M	61.0	1030	2	86.83	46.00	7.83	4.17	0	
M08-24	Mountain	M	62.9	1000	1	89.34	49.77	8.02	4.78	3	
M08-25	Mountain	F	57.8	750	1	81.18	45.77	7.76	3.99	2	
	Lowland $\bar{x}$		59.6	807.5	1.5	84.77	47.95	7.58	3.99	2.40	2.11
	Mountain $\bar{x}$		59.7	812.8	1.8	84.35	45.68	7.70	4.11	1.62	0.50
	Grand $\bar{x}$		59.7	807.0	1.7	84.49	46.45	7.66	4.07	1.88	1.35
	Yom-Tov (2008) $\bar{x}$					82.26	49.97	8.45	4.32		

[a] Body length measured from end of nose to tip of tail.

[b] Body weight did not include pelts.

[c] Greatest length of skull

[d] Greatest zygomatic breadth

[e] Greatest length of fourth upper premolar

[f] Greatest width of upper canine