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Abstract

Mesocarnivores are increasingly recognized as key drivers of community dynamics, but the effects of bottom-up and abiotic factors on mesocarnivore populations remain poorly understood. We evaluated the effects of snow conditions, prey abundance, and habitat type on the distribution of five sympatric mesocarnivore species in interior Alaska using repeated snow track surveys and occupancy modelling. Snow depth and snow compaction were the best predictors of mesocarnivore occupancy, with differential effects across species. Coyotes (*Canis latrans* (Say, 1823)) and red foxes (*Vulpes vulpes* L., 1758) occurred in areas of shallow, compact snow, Canada lynx (*Lynx canadensis* (Kerr, 1792)) occurred in areas of shallow, fluffy snow, and wolverines (*Gulo gulo* L., 1758) and marten (*Martes americana* (Turton, 1806)) occurred in areas of deep, fluffy snow. These findings indicate that altered snow conditions due to climate change may have strong direct effects on the distribution of northern mesocarnivores, with divergent effects across species.

Keywords: climate change, furbearer, habitat, mesopredator, snow depth, species distribution, coyote, *Canis latrans*, red fox, *Vulpes vulpes,* Canada lynx, *Lynx Canadensis*, wolverine, *Gulo gulo*, marten, *Martes americana.*

Introduction

Interspecific interactions between meso- and apex predator species, and the resulting impacts on lower trophic levels, have been well documented and highlight the profound impact carnivores can have at a community scale (e.g., Crooks and Soule 1999; Prugh et al. 2009; Roemer et al. 2009; Levi and Wilmers 2012). Most studies of mesocarnivores have focused on these intraguild interactions, whereas fewer studies have investigated the effects of bottom-up and abiotic factors, such as snow conditions and habitat characteristics, on their dynamics (e.g., Rose and Polis 1998, Riley et al. 2003; Bateman and Fleming 2012). These factors are particularly important to investigate in regions that are experiencing large scale environmental change.

The boreal ecosystem represents the world's largest terrestrial biome and harbors a diverse community of mesocarnivores throughout its circumpolar distribution (Olsson 2009). However, boreal ecosystems are among the most vulnerable to climate and anthropogenic induced change, and mesocarnivores inhabiting these environments may be strongly affected by habitat loss, changing prey dynamics, and major climate shifts (Cameron et al. 1992; Amstrup 1993; Marcot et al. 2015). Furthermore, increases in human activity and habitat disturbance due to energy exploration may lead to major landscape level changes in this region (Johnson et al. 2005). Understanding the effects of bottom-up and abiotic factors on boreal mesocarnivore space use is necessary to effectively manage these species as conditions rapidly change.

We examined how snow conditions, habitat type, and prey abundance influenced winter occupancy patterns of coyotes (*Canis latrans* (Say, 1823)), red foxes (*Vulpes vulpes* L., 1758), Canada lynx (*Lynx canadensis* (Kerr, 1792)), wolverines (*Gulo gulo* L., 1758), and marten (*Martes americana* (Turton, 1806)) in interior Alaska. We used occupancy modelling, which uses repeated presence-absence survey data to estimate detectability and space use patterns, to test predictions about the effects of these bottom-up and abiotic factors on mesocarnivore

populations (MacKenzie et al. 2002). Food abundance during winter months has been shown to strongly impact the reproductive success of some mesocarnivores (Angerbjörn et al. 1991; Persson 2005). Climate change is predicted to have especially strong effects on winter conditions in Alaska, with major impacts on snow characteristics (SNAP 2015). Snow characteristics such as depth and compaction (i.e., hardness) can strongly affect the energetics of locomotion, foraging efficiency, and predation risk of animals (Gese and Grothe 1995; Crête and Larivière 2003; Thibault and Ouellet 2005). Although the diet and space use of sympatric mesocarnivores can overlap substantially (Ruggiero et al. 1994; Riley et al. 2003; Schuette et al. 2013; Goad et al. 2014), interspecific differences may lead to divergent effects of abiotic and biotic factors across species. The relative importance of these factors to different species of mesocarnivores remains unclear, because most studies have focused on one or a few species rather than the entire guild.

We predicted that snow depth (total accumulated snowfall) and snow compaction (the firmness of snow) would have strong influences on mesocarnivore occupancy. We expected snow depth to negatively affect coyotes and red foxes and have a neutral or positive influence on lynx, marten, and wolverines. Deep snow can hinder most species' ability to effectively move and forage, but the low foot-load of lynx (4.1-8.8 times less than that of coyotes) enables them to move on top of the snow where other species will sink in (Halpin and Bissonette 1988; Murray and Boutin 1991). Similarly, mustelids are able to use their long body and short legs to increase surface area and avoid sinking into deep snow (Raine 1983). Although coyotes have been shown to adapt to high-elevation, deep snow conditions in northwestern Wyoming, USA (Dowd et al. 2013), we expected both canid species would prefer areas with shallow snow in our study region characterized by fine-scale variability in snow depth. Further, we expected snow compaction to positively affect coyotes and foxes. Compact snow allows canids to move across the landscape quickly, aiding in their ability to avoid competitors and increasing their effectiveness as coursing predators (Murray and Boutin 1991). Snow that becomes crusted and compact due to wind or freeze-thaw cycles can aid in red fox movement (Halpin and Bissonette 1988) and we expected to see this pattern for both canid species in our study.

We predicted that habitat would also strongly influence mesocarnivore occupancy at the guild level, and that species-specific differences in habitat affiliation would occur. Coyotes and red foxes, along with wolverines, are considered habitat and foraging generalists in northern regions, which aids in their adaptability to a variety of environmental conditions (Kamler and Gipson 2000; Grinder and Krausman 2001; Kilström 2004; Perrine 2005). Marten are also able to exploit a wide range of prey resources, but they are fairly restricted to mature forest habitat (Zielinski et al. 2005). Lynx, perhaps one of the best examples of a predatory specialist, are well known for their dietary dependence on snowshoe hares (*Lepus americanus* (Erxleben, 1777)) and are therefore associated with mature or mixed-age forest and tall shrub habitats that support hares (Ruggiero et al. 2000; Feierabend and Kielland 2015). For specialist species (lynx and marten), we expected relatively high occupancy probabilities in forested habitats based on their prey requirements and species behaviour (Ruggiero et al. 2000; Zielinski et al. 2005). For generalist species (wolverine, coyote and fox), we did not expect to find differences in occupancy based on habitat type because these species are well adapted to a variety of habitats.

Finally, we predicted that prey abundance would be a strong predictor of overall mesocarnivore occupancy, and that mesocarnivore species other than wolverine would have positive responses to areas with high small mammal prey abundance. Lynx, marten, coyotes, and red foxes have all been shown to prey upon a variety of small mammal prey items (e.g.; Zielinski et al. 2005; Jankowiak et al. 2008; Prugh et al. 2008) and considerable overlap in mesocarnivore diet has been observed in our study region (Sivy 2015). Therefore, we expected that areas with relatively abundant small mammal prey would have higher occupancy probabilities for those mesocarnivores. Wolverines are known to scavenge heavily on carrion during winter months and depend less on small prey such as hares and voles (Lofroth et al. 2007; Dalerum et al. 2009). For this reason, we predicted that our measure of small prey abundance would not influence wolverines' occupancy to the same degree as the other mesocarnivore species.

Materials and methods

Study Region

Our study region included two study sites (hereafter, "Denali" and "Susitna") within the central Alaska Range of interior Alaska (Fig. 1). Boreal forest (including spruce *Picea spp.*, aspen *Populus spp.* and birch *Betula spp.*), deciduous shrub, and tundra habitats dominate the landscape across both sites. This region is characterized by short summers and long, cold winters with ground-covering snow that can last from September until May (Shulski and Wendler 2007). Wolves (*Canis lupus* L., 1758), black bears (*Ursus americanus* (Pallas, 1780)) and grizzly bears (*Ursus arctos* L., 1758) were present in the region, as well as caribou (*Rangifer tarandus* L., 1758) and

moose (*Alces alces* L., 1758). The Denali study site was a 2000-km^2 area made up of federal, state, and private lands including the north-eastern portion of Denali National Park and Preserve (DNPP) along with portions of the Stampede corridor, a 470-km^2 parcel of state and private land. The Susitna study site was approximately 145 km southeast of the Denali study site and consisted of 1,800 km^2 of primarily public (state and Bureau of Land Management) or Alaska Native corporation lands.

Survey Methods

We used a grid-based sampling design to collect data on mesocarnivore presence, prey abundance, snow depth and compaction, and habitat characteristics within our study region. We used ArcGIS (version 10.1, ESRI, Redlands, California) to overlay each study area with a grid of 2-km by 2-km cells. This cell size (4 km^2) was chosen because it most closely matched the home range size of marten, the smallest of our target species (Buskirk 1983). Analysis at this spatial scale represented true occupancy probability for marten, but the assumption of spatial closure was likely violated for the other species. Thus, "occupancy probabilities" corresponded to probabilities of use for foxes, coyotes, lynx, and wolverines. For simplicity, however, we refer to these as "occupancy probabilities" for all species. We assigned each grid cell one of three habitat types (forest, shrub, or tundra) based on the dominant vegetation cover type within the cell, as calculated from satellite imagery (National Land Cover Database 2001).

Surveys were conducted by two researchers within each study site from approximately 01-Jan-2013 to 31-Mar-2013 and 01-Jan-2014 to 31-Mar-2014. A stratified random sample of cells was selected from each study site based on the proportion of cells within each habitat classification. In 2013, we evaluated the efficacy of three survey techniques: linear transects ($n = 51$ cells), square transects ($n = 39$ cells), and remote cameras ($n = 45$ cells). Cameras provided too few photos, and these cells were excluded from analyses. The linear transect method used temporal replication to estimate detection probabilities, whereas the square transects used spatial replication, which eliminated the need for return visits to the cell (MacKenzie et al. 2006). Where terrain allowed and snowmobile use was permitted, cells were surveyed by snowmobile. Where snowmobile use was prohibited (i.e., designated wilderness areas in DNPP) or impractical due to terrain, we surveyed linear transects by dog team or on foot. Areas surveyed by dog team were frequented by other dog mushers as well. Square transects were 1 km on each side and surveyed in a single visit. Linear transects were 1.87 km long on average (SE = 0.063), and they were surveyed repeatedly throughout the winter (range = 2-10 repeats, mean = 3.88). In 2014, we re-surveyed the randomly generated cells from 2013 and also surveyed those cells that we travelled through en route to the random cells (Fig. 1). All cells in 2014 (n=210) were surveyed using linear transects with temporal replication. This design increased our sample size and survey efficiency.

For all transects, we recorded all target mesocarnivore tracks encountered during the survey. For each carnivore track encountered, we identified it to species and marked the location on a handheld GPS unit (Garmin eTrex30, Garmin Ltd.). We tallied the number of ptarmigan (*Lagopus spp* (Brisson 1760)) and grouse (*Falcipennis canadensis* L., 1758), snowshoe hare, red squirrel (*Tamiasciurus hudsonicus* (Erxleben 1777)) and vole (Cricetidae family (Fischer 1817)) tracks encountered at 500-m intervals during each survey to establish an index of small prey use in each survey cell.

We recorded snow depth and snow compaction at the start of each transect and every 500 m thereafter. Because snow conditions can affect detection probability, we conducted surveys after a minimum of 24 h since the last track-obliterating snowfall to allow adequate time for tracks to accumulate, and no more than 7 days after a snowfall to prevent tracks from becoming too degraded. Snow compaction was indexed by measuring the sink depth of a 200-g penetrometer (diameter = 8.2 cm and height = 4.2 cm), dropped from 50 cm above the ground (sensu Whiteman and Buskirk 2013). Snow depth and compaction were also recorded at each encountered mesocarnivore track, along with the sink depth of a randomly-selected paw print (measured from the center of the pad) to assess the relationship between snow conditions and each species' sinking depth. We used a one-way analysis of variance (ANOVA) to test for difference in sink depths among mesocarnivore species. We used the log ratio of track sink depth to snow compaction as our response variable to control for the effect of snow compaction on sink depth. We used the Tukey Honestly Significant Difference test to examine pairwise differences among species.

Occupancy Analysis

We used single-season occupancy models to estimate occurrence (use) probabilities of the target mesocarnivore species. The single-season occupancy model provides estimates of two response parameters: probability of site occupancy (ψ), and detection probability (p), which is the probability that the target species tracks are detected

given that it is present (MacKenzie et al. 2002). Although two seasons of data were included in our analysis, we used a single-season model framework and included year as a covariate in our candidate model set because we were most interested in factors affecting use, not occupancy dynamics that would require estimation of colonization and extinction parameters. Similarly, species was included as a covariate, which allowed us to combine data from all species into one database and develop models to examine species-specific differences as well as guild-wide patterns. All analyses were performed in program R version 3.1.0 (R Development Core Team 2014) using packages unmarked (Fiske and Chandler 2011) and AICcmodavg (Mazerolle 2015).

We included two survey-specific covariates and eight site-specific covariates in our models using a logit link function. Survey covariates were: number of days since the last snowfall (DSLS) and total distance (km) surveyed within a sample cell (DIST). Site-specific covariates were: study year (YEAR), survey method (METHOD), study area (AREA), habitat type (HABITAT), species (SPECIES), average snow depth over all survey occasions (DEPTH), average snow compaction over all survey occasions (COMPACTION), and average total combined prey species abundance per km surveyed, adjusted for days since last snowfall (PREY). We calculated PREY by summing the tracks in a given cell on a given survey and then dividing by the distance surveyed in that cell (because cells varied in km surveyed per cell). This value was then multiplied by the number of days since last snowfall to account for accumulation over time. We calculated average snow depth, snow compaction, and prey abundance within each habitat type and used a Pearson's correlation matrix to test for correlations among continuous covariates. DSLS, DIST, DEPTH, COMPACTION, and PREY were standardized for analyses.

We used a three-step process to develop a finalized candidate model set that was both biologically relevant and analytically feasible. We ranked all models based on AICc and QAICc (Burnham and Anderson 2002). First, we constructed models to estimate p while holding ψ constant (Schuette et al. 2013), using all combinations of DSLS, DIST, YEAR, METHOD, AREA, and SPECIES. The top-ranking model contained DSLS, DIST, AREA, and SPECIES, and received 37% AICc weight. The next best model contained DSLS, DIST, YEAR, AREA, and SPECIES and received 32% AICc weight. Both models received significant support (Δ AICc < 1), therefore we used all covariates from the more parameterized model, p(DSLS+DIST+YEAR+AREA+SPECIES), in the next steps in order to account for all relevant predictors of p.

In the second step, all combinations of YEAR, AREA, HABITAT, SPECIES, DEPTH, COMPACTION, and PREY were used to build models that estimated ψ while p was modelled as a function of covariates from step one. This resulted in a full candidate set of 128 additive models. We used this full set of models to calculate summed individual covariate weights to assess the relative importance of each predictive covariate on guild-wide occupancy. Covariates with weights > 50% were considered important (Burnham and Anderson 2002). In step three, we used a Δ AICc $\leq$ 2 cut-off to reduce the full candidate set to the top 9 models. We supplemented this model set with six interaction models and a null model, for a final candidate model set of 16 models. Each of these six models contained an interaction term between SPECIES and one of the other six covariates used to model occupancy. These models were developed to directly address species-specific predictions about the influence of snow, habitat type and prey on occupancy.

We assessed model fit by evaluating the most complex model in the candidate set using a Pearson χ^2 goodness-of-fit test (MacKenzie and Bailey 2004) in package AICcmodavg with 1,000 bootstrapped simulations. We used an estimate of the overdispersion factor ($\hat{c}$) to evaluate the dataset and identify potential overdispersion or independence violations. Violating the assumption of independence can lead to spatial autocorrelation issues and result in overly precise variance estimates (MacKenzie et al. 2006). We found a $\hat{c}$ value of 1.87, suggesting reasonable fit, and we therefore used the quasi-corrected AICc (QAICc) to rank the final 18 model set. In addition, we used the estimate of $\hat{c}$ to inflate standard errors to account for overdispersion (Burnham and Anderson 2002).

Species-specific occupancy and detection probability estimates were generated from the best-supported model (lowest QAICc) in the final 16-model set. We addressed our predictions by describing the influence of each explanatory covariate on guild-wide mesocarnivore occupancy using summed AICc weights from the full, additive model set, and we addressed species-specific occupancy predictions using the final model set with interaction terms.

Results

Both snow characteristics, DEPTH and COMPACTION, strongly influenced guild-wide mesocarnivore occupancy as well as species-specific occupancy probabilities. Snow DEPTH and COMPACTION received 55.5% and 68.2% AICc support weight in the additive model set (Table 1), and the top two models in the final 16-model set (which had a combined 92.1% QAICc weight) both estimated occupancy as a function of species and snow condition interactions (Table 2).

Overall occupancy (i.e., the proportion of survey cells across both areas that were occupied or used; ($\psi \pm$ SE)) was highest for wolverines (0.62 $\pm$ 0.09) and lowest for marten (0.19 $\pm$ 0.04). Coyotes (0.36 $\pm$ 0.05), red foxes (0.50 $\pm$ 0.05), and lynx (0.45 $\pm$ 0.07) had similar, intermediate occupancy probabilities. We used our top-ranking model (ψ(SPECIES*COMPACTION) to produce these estimates while holding COMPACTION at its mean value. Detection probabilities ($p \pm$ SE) from this top ranking model were greatest for red foxes in Susitna during 2013 (0.40 $\pm$ 0.05) and lowest for wolverines in Denali in 2014 (0.13 $\pm$ 0.03). Overall, detection probabilities were lower in Denali than Susitna (Fig. 2). Detection probability (logit-transformed model coefficients $\pm$ SE) was lowest during the 2014 survey season (β = -0.13 $\pm$ 0.13).

We predicted that snow depth would negatively impact all canids, and have a neutral or positive impact on lynx and the mustelids. Indeed, areas with deeper snow were less likely to be occupied by coyotes (β = -0.28 $\pm$ 0.20) and red foxes (β = -0.21 $\pm$ 0.27), but they were also less likely to be occupied by lynx (β = -0.57 $\pm$ 0.37). Areas with deeper snow were more likely to be occupied by wolverines (β = 0.96 $\pm$ 0.33) and marten (β = 1.27 $\pm$ 0.36; Fig. 3 A). Coyotes (β = -0.23 $\pm$ 0.19) and red foxes (β = -0.16 $\pm$ 0.27) had higher occupancy probabilities in areas with compact snow, whereas lynx (β = 0.83 $\pm$ 0.33), wolverine (β = 0.88 $\pm$ 0.33), and marten (β = 1.44 $\pm$ 0.37) had higher occupancy probabilities in areas with fluffy snow (Fig. 3 B). Average (mean $\pm$ SE) sink depth of snow tracks was greatest for lynx (6.3 cm $\pm$ 0.3) and wolverines (6.5 cm $\pm$ 0.3) and lower for coyotes (4.5 cm $\pm$ 0.2), red foxes (4.1 cm $\pm$ 0.2), and marten (4.4 cm $\pm$ 0.2). Species differed in sink depths when controlling for snow compaction ($F_{4,802}$ = 78.55, p < 0.001). After accounting for snow compaction, average (mean $\pm$ SD) backtransformed sink depth: snow compaction ratios indicate coyotes (1.1 $\pm$ 0.9) had the highest foot-load ratio and marten (0.5 $\pm$ 0.2) had the lowest. Pairwise species comparisons indicated that marten had significantly lower sink depths (p < 0.00) when accounting for snow compaction that coyotes, red foxes, wolverines, and lynx. Coyote sink depths were marginally greater than red foxes (p = 0.02), and no other significant differences existed between species.

Snow depths (mean $\pm$ SE) were similar in shrub (44.2 $\pm$ 1.8) and forest (39.0 $\pm$ 2.1) habitats and lowest in tundra (28.4 $\pm$ 2.2). Compaction was greatest (least penetrable snow) in the tundra (4.9 $\pm$ 0.3) and least (most penetrable snow) in the forest (8.0 $\pm$ 0.3). The correlation between both snow characteristics (DEPTH and COMPACTION) and PREY was low (-0.19 and -0.22, respectively). Prey abundance was highest in forest habitats (7.6 $\pm$ 1.5 tracks per km*day), moderate in shrubs (3.2 $\pm$ 0.4), and lowest in tundra (1.8 $\pm$ 0.2).

We predicted HABITAT would be an important explanatory covariate of guild-wide as well as species-specific mesocarnivore occupancy. Our full model set indicated that HABITAT was indeed the most influential variable on guild-wide occupancy (Table 1). Based on model ψ(HABITAT+SPECIES), probability of occupancy (logit-transformed model coefficients $\pm$ SE) was highest in the forest (β = -0.05 $\pm$ 0.28) and lowest in the open tundra landscapes (β = -1.27 $\pm$ 0.27) across all species. We also predicted that specialist species would prefer forested habitats whereas generalists would show little preference among the three major habitat types. Model ψ(HABITAT*SPECIES) revealed that lynx and marten (known habitat specialists) indeed had highest occupancy probabilities in forested habitat and the remaining species (habitat generalists) had more equally distributed occupancy probabilities among the three habitat categories, but patterns of habitat use across all species were quite similar (Fig. 4). Although habitat strongly influenced guild-wide mesocarnivore occupancy, the ψ(HABITAT*SPECIES) model had little support (Δ QAICc > 12.0), indicating that other factors had stronger effects on species-specific spatial patterns.

Lastly, PREY was a poor predictor of guild-wide mesocarnivore occupancy (Table 1). The influence of PREY on mesocarnivores at the species-specific level was assessed in model ψ(SPECIES*PREY) (Table 2). Probability of occupancy (logit-transformed model coefficients $\pm$ SE) increased in areas of greater prey abundance for coyotes (β = 0.71 $\pm$ 0.33), lynx (β =5.52 $\pm$ 2.83), and wolverines (β = 2.21 $\pm$ 1.70), and decreased with greater prey abundance for red foxes (β = -0.90 $\pm$ 0.38) and marten (β = -1.33 $\pm$ 0.53). However, this model received little support (QAICc weight = 3%).

Discussion

Our analysis of northern mesocarnivore occupancy indicates that abiotic factors can strongly affect this important guild. Snow depth and compaction were the most influential predictors of mesocarnivore occupancy that we examined. The negative response to increasing snow depth shown by coyotes and red foxes matched our predictions. Likewise, we found that these species were more likely to occur in areas of more compact snow. Wind-blown regions, river corridors, existing animal travel routes, roads, and trails are all areas that could produce highly compacted and relatively shallow snow conditions, and these areas can allow canids to more successfully chase prey, escape predators by using familiar travel routes, and increase visibility to aid in hunting and predator avoidance (Murray and Boutin 1991; Murray et al. 1994).

We predicted that lynx, unlike canids, would be more tolerant of deep snow conditions due to their low foot loading (Murray and Boutin 1991; Murray et al. 1994). Surprisingly, lynx occupancy was lowest among all study species in areas of deep snow. However, their high occupancy probability in areas of less compact (fluffy) snow suggests that lynx were most frequently using areas with shallow, but fluffy snow. Like canids, lynx may use shallow snow to reduce energetic costs, and lynx have been shown to avoid areas with compact snow to avoid competitive interactions with canids (Ruggiero et al. 2000). We found that lynx tracks sank into snow more deeply than either canid species, contrary to our expectations based on foot-load ratios (Murray and Boutin 1991; Murray et al. 1994). However, lynx had higher probability of use in areas with fluffy snow, which could lead to a deeper sink depth than canids without increasing energetic costs. Canid sink depth was likely reduced relative to lynx due to their higher use of compacted snow areas. Indeed, when we accounted for snow compaction using log ratios, we found that coyotes had a higher ratio of track depth to snow compaction than lynx (0.0 and -0.5, respectively).

We found that snow characteristics were better predictors of landscape-scale occupancy than either prey abundance or habitat type, although we recognize that we measured snow conditions and prey abundance at a finer resolution than habitat type. Lynx are generally thought to use areas where they can most successfully access their primary prey source, with snow conditions playing a minimal role in use patterns (Ruggiero et al. 2000). Lynx are suited to hunt in a variety of snow conditions because they can hunt effectively with either a chasing or ambushing strategy, in contrast to coyotes, which change their hunting behaviour from chasing to a less familiar ambushing approach in deep snow (Murray and Boutin 1991; Murray et al. 1995). The highest prey abundance during our study occurred in forested areas with fluffy snow, two conditions that were associated with high probabilities of lynx use. We recognize that it may be hard to distinguish between primary drivers of habitat selection when a species uses two spatially correlated resources. However, snow conditions and prey abundance were not correlated in our study, and snow depth did not differ between forest and shrub habitats. In addition, lynx space use patterns may be determined primarily by snow conditions when there is an increased need for long distance daily travel. This need can occur during periods of low snowshoe hare abundance (Ward and Krebs 1985), as was the case during our study (Krebs et al. 2013).

Mustelids also had highest probabilities of occupancy in areas of fluffy snow, but they were more likely to occur in areas with deeper snow. Marten in Manitoba were found to occur across a range of snow depths and were seemingly unaffected by deep snow, possibly using subnivean travel routes under deep snowpack for thermal cover, predator avoidance, and increased access to prey species such as voles (Raine 1983). However, subnivean travel can also be energetically costly and marten are known to frequent subnivean areas in deep snow as simple resting sites (Wilbert et al. 2000). Similarly, wolverines are known to require persistent spring snow for denning (McKelvey et al. 2011), which may explain their occurrence in deep snow areas throughout the winter leading up to the denning period. Although it is possible that marten use of deep, fluffy snow was a consequence of avoiding larger mesocarnivores that preferred shallow snow (Lindström et al. 1995; Bull and Heater 2001; Sivy 2015), wolverines were the largest mesocarnivores in our analysis, and their movements were unlikely driven by avoidance behaviour.

Snow conditions strongly affected occupancy of all mesocarnivores in our study, and yet those effects varied substantially among species. Climate change may directly impact these species' space use patterns, and ultimately their distribution. Snow conditions in northern boreal regions of Alaska, and worldwide, are predicted to change dramatically over the next century (Chapin et al. 2014; Winfree et al. 2014). Warmer temperatures and increased precipitation throughout the winter months may increase the variability of climatic conditions across the boreal regions. Areas projected to warm above freezing may experience more rain, less total snow accumulation, and wetter snow that more easily becomes compacted. In those regions, species that use areas with shallow, compacted snow (i.e. canids) may become more widespread and abundant due in part to energetically efficient travel, increased hunting opportunities, and easier predator avoidance. In areas projected to remain below freezing,

increases in winter precipitation could increase snow depth, which may favor mustelids by increasing access to spring denning areas and allowing for more consistent subnivean travel corridors. Snow conditions in boreal regions are projected to become similar to current conditions in areas such as the northwestern United States, where mid-elevation mountainous regions experience more winter precipitation as snow, and lower or more coastal regions receive more rain (McKelvey et al. 2011; SNAP 2015). Our study was conducted near the northern edge of the region that harbors all five of our studied mesocarnivore species, with the southern edge of this region extending into the northwestern United States (US). Although the northwestern US does contain viable wolverine, marten, and lynx populations, these populations are generally restricted to isolated boreal regions with deep, persistent snow cover (Ruggiero et al. 1994). In contrast, coyotes and red foxes are widespread throughout North America, including areas that receive little or no snow (Riley et al. 2003). Canids in northern boreal regions may therefore adapt more easily than mustelids to future changes in snow characteristics.

Surprisingly, habitat was a poorer predictor of species-specific occupancy probabilities than snow conditions. Thus, the effect of habitat type on occupancy does not appear to vary substantially among species. However, habitat was a strong predictor of occupancy when examining all mesocarnivores together, and we found forest habitat types to be areas of highest occupancy probabilities. The latter results are consistent with previous findings, especially those describing lynx and mustelid habitat use (e.g., Ruggiero et al. 1994; Kilström 2004; Squires et al. 2010).

We found highest numbers of prey in forest habitats, which could explain higher levels of mesocarnivore use in forested areas. However, we did not find prey abundance to be a strong predictor of occupancy in any analyses. Prey tracks may be a poor index of abundance, especially for species such as voles that can travel below the snow or for highly wind disturbed areas. Precise, spatially-explicit estimates of prey abundance can be difficult to obtain across large study areas required for carnivore studies. Track counts provide a spatially-explicit abundance index that has been used in numerous studies worldwide (Thompson et al. 1989; Vigeant-Langlois and Desrochers 2011; Kawaguchi et al. 2015), but validation of this method is needed before strong conclusions can be drawn. Future research testing the validity of track counts as indices of prey abundance would greatly improve our ability to examine the relative importance of prey availability across large regions.

Occupancy models based on snow track data facilitate a multi-species approach, but differences among species in home range sizes complicates the selection of a sampling grid cell size. We selected a cell size ($4km^2$) that represented the average home range for marten in our study area (Buskirk 1983), because marten had the smallest home range size among the species in our study. Our estimated occupancy probabilities for marten therefore represented "true" occupancy (i.e., the probability that a given cell is occupied by the species). However, individuals of other species likely ranged over multiple cells, violating the assumptions of independence and closure (Mackenzie et al. 2002). Occupancy probabilities for these species are thus more appropriately interpreted as probabilities of use (Mackenzie et al. 2002). For example, wolverines in boreal regions similar to our study area have been documented to have home ranges up to 2563 km^2 (Dawson et al. 2010). Concurrent genetic analyses of hair and feces collected in our Susitna study area identified 9 unique individual wolverines (Alaska Energy Authority 2015), indicating home ranges may have been smaller in our study region or wolverine home ranges overlapped substantially. Although caution is needed when interpreting occupancy probabilities in cases where assumptions are violated, these estimates are useful in examining patterns of space and resource use.

In conclusion, our study indicates that snow conditions likely play a large role in determining guild-wide and species-specific patterns of mesocarnivore occupancy in northern boreal regions. It is likely that there will be winners and losers when it comes to adapting to landscape level changes, and we have shown that snow conditions, which are likely to change dramatically in the near future, may be one of the most significant factors determining who wins and who loses. In addition to direct impacts on mesocarnivore distributions, changing snow conditions may indirectly affect mesocarnivores by altering outcomes of intraguild interactions. In turn, the shifting mesocarnivore guild may lead to further cascading effects on prey communities. Future work should explore the impact of snow conditions on mesocarnivore occupancy over time and across a wider range of boreal environments to assess how patterns of use change with a changing climate. In addition, addressing the link between these abiotic drivers and interspecific interactions may help to further understand space use patterns.

Acknowledgements

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Tables

Table 1. Influence of covariates (summed AICc weight) on mesocarnivore occupancy probabilities in interior Alaska, 2013-2014. Levels of each categorical covariate are listed in the description.

Covariate Name	Description	AICc Weight (%)
SPECIES	Target species (coyote, lynx, marten, red fox, wolverine)	99.9
HABITAT	Major habitat type within sample cell (forest, shrub, tundra)	99.2
COMPACTION	Survey cell average snow compaction. Standardized to mean of 0	68.2
DEPTH	Survey cell average snow depth. Standardized to mean of 0	55.5
PREY	Average prey species abundance per cell. Standardized to mean of 0	40.5
AREA	Study site (Denali or Susitna)	34.7
ACTIVITY	Level of anthropogenic activity within cell (high or low)	29.2
YEAR	Study year (2013 or 2014)	27.8

Table 2. Top ranked models explaining mesocarnivore occupancy in interior Alaska, 2013-2014. Models are described by the number of parameters (*K*), Quasi-Akaike Information Criterion value corrected for sample size (QAICc), change in QAICc (Delta_QAICc) and overall model weight (QAICcWt). Models represent the subset with Δ QAICc < 10 from the final set of 18 models. The detection probability, *p,* was modeled as *p*(AREA+DIST+DSLS+SPECIES+YEAR) for all 8 models.

Model Description	*K*	QAICc	Delta_QAICc	QAICcWt
ψ(SPECIES*COMPACTION)	20	1537.39	0.00	0.58
ψ(SPECIES*DEPTH)	20	1538.48	1.09	0.34
ψ(SPECIES*PREY)	20	1543.15	5.76	0.03
ψ(HABITAT+SPECIES)	17	1545.40	8.01	0.01
ψ(HABITAT+SPECIES+COMPACTION)	18	1546.02	8.63	0.01
ψ(HABITAT+SPECIES+SNOW)	18	1546.71	9.31	0.01
ψ(SPECIES*AREA)	20	1546.71	9.32	0.01
ψ(HABITAT+SPECIES+SNOW+COMPACTION)	19	1546.84	9.45	0.01

Figure legends

Figure 1. Interior Alaska mesocarnivore study region and survey locations including individual 2 x 2 km survey cells (*n* = 300). White cells were surveyed during 2013, black cells were surveyed during 2014, and cross-hatch cells were surveyed both years.

Figure 2. Detection probability estimates with standard errors for each target species by study site in 2013. Estimates were derived from the top ranking overall model: ψ(SPECIES*COMPACTION) *p*(AREA+DIST+DSLS+SPECIES+YEAR). DIST and DSLS were held at their mean value.

Figure 3. Occupancy probability for each target species based on snow conditions within the interior Alaska study region, 2013-2014. (A) Snow depth and (B) snow compaction are measured in cm. Snow compaction ranges from highly compact (0) to fluffy (10). Error bands represent 95% confidence intervals.

Figure 4. Species-specific occupancy probabilities across major habitat categories within the interior Alaska study region, 2013-2014. Error bars represent 95% confidence intervals.
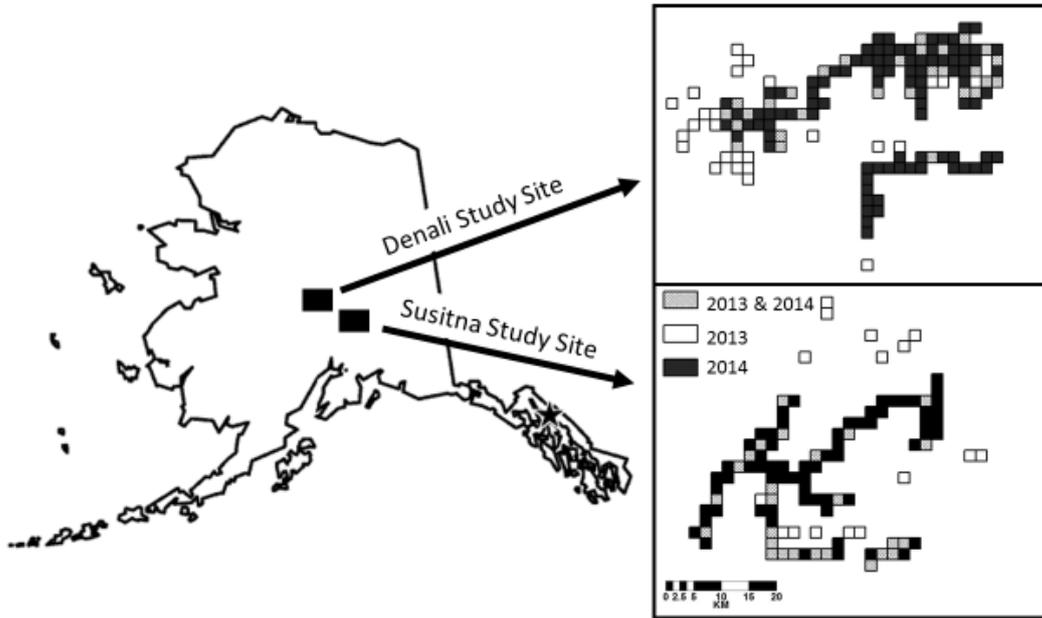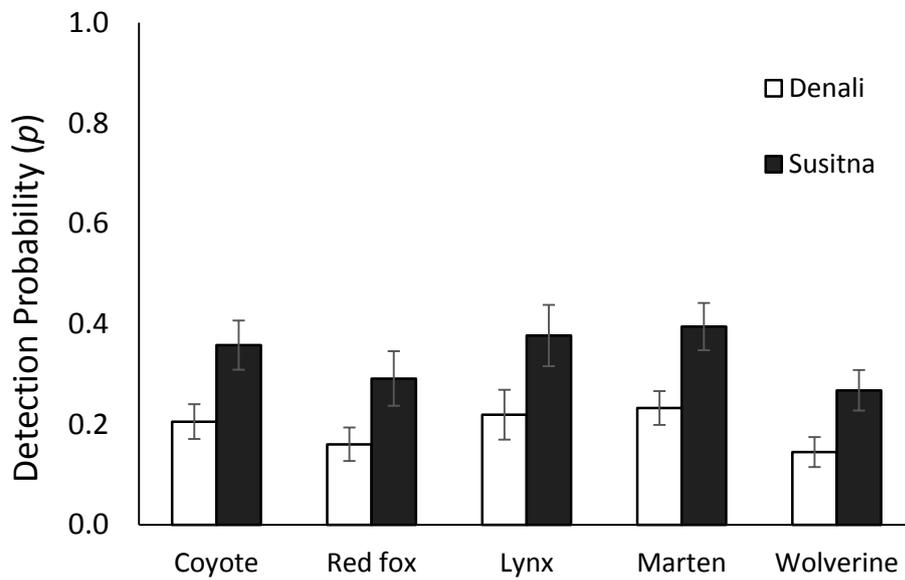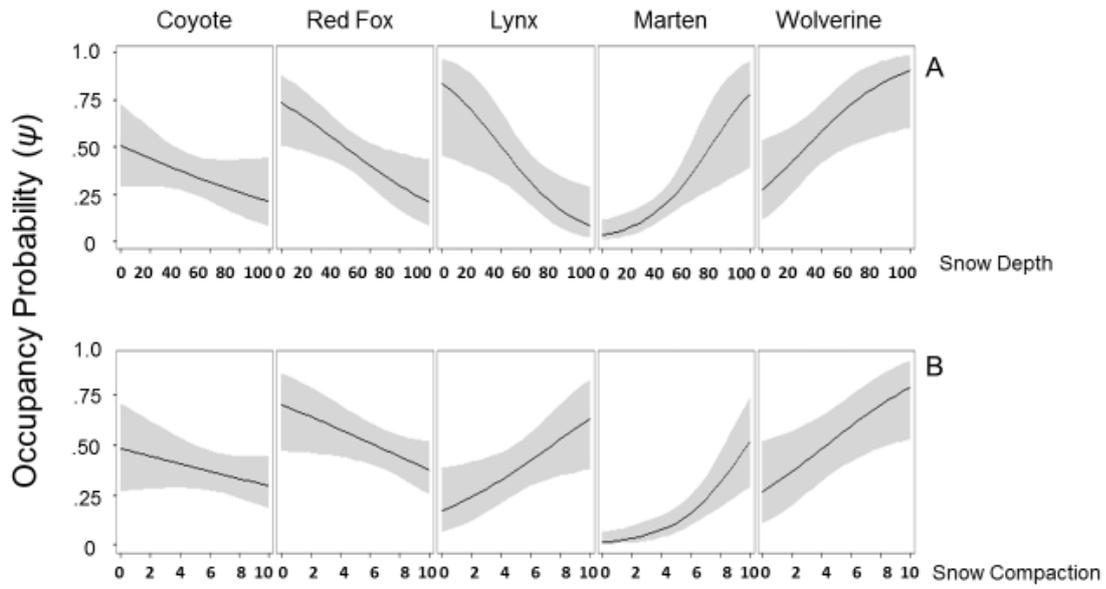
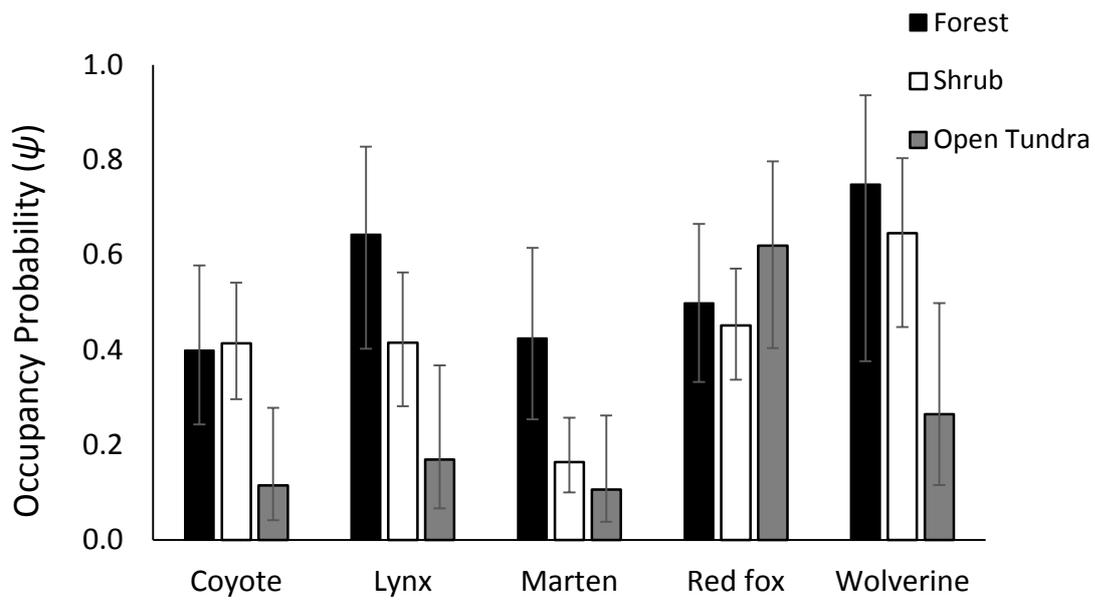**Figures**

Figure 1.

Figure 2.

Figure 3.

Figure 4.