

Influence of spatial variation in forage availability and predation risk on habitat
selection by woodland caribou (*Rangifer tarandus caribou*) in Ontario

by

Madeleine McGreer

A Thesis
presented to
The University of Guelph

In partial fulfillment of requirements
for the degree of
Masters of Science
in
Integrative Biology

Guelph, Ontario, Canada

© Madeleine McGreer, October, 2014

ABSTRACT

INFLUENCE OF SPATIAL VARIATION IN FORAGE AVAILABILITY AND PREDATION RISK ON HABITAT SELECTION BY WOODLAND CARIBOU (RANGIFER TARANDUS CARIBOU) IN ONTARIO

Madeleine McGreer
University of Guelph, 2014

Advisor:
Professor J. M. Fryxell

Little is currently known about how selection for particular habitats relates to fitness constraints, nor how the strength of selection for specific fitness metrics changes due to variation in habitat availability across broad landscape gradients. I examine site selection by 110 woodland caribou equipped with GPS radio-collars with respect to two fitness-related metrics, forage availability and predation risk, across a broad spatial gradient of forage and risk availability. I found that caribou select habitats that reduce predation risk and improve access to forage. By comparing within-population variation in forage availability and risk prevalence, I found that caribou face a forage-risk trade-off in summer but not winter. Caribou decreased selection strength for forage with forage availability in winter, but not summer. In contrast, caribou in both seasons increased risk avoidance in riskier ranges. These findings suggest that trade-offs other than food versus safety influence caribou habitat use decisions.

ACKNOWLEDGEMENTS

These data were gathered as part of a multi-agency project involving collaboration between researchers at the University of Guelph lead by Dr. John Fryxell and researchers from the Wildlife Research and Development Division and the Center for Northern Forest Ecosystem Research of the Ontario Ministry of Natural Resources (Dr. Ed Iwachewski, Dr. Ian Thompson, Dr. Arthur Rodgers, Dr. Jen Schuter, Dr. Glen Brown, Dr. Douglas Reid, Jevon Hagens, and Philip Wiebe), as well as researchers at the University of Trent lead by Dr. Brent Patterson, and Erin Mallon, advised by Merit Turetsky at the University of Guelph. Without all the members of this large collaboration, I would not have any data with which to write a thesis.

I would like to thank my advisor John Fryxell, for his advice, and for keeping me on track over the past two years. I would also like to thank my committee members, Ryan Norris and Rob Deardon, for their guidance and support. Rob Deardon, in particular, offered me invaluable statistical advice. I'd like to thank the past and present members of my lab, Dr. Anna Mosser, Dr. Tal Avgar, Andrew Kittle, Garrett Street, Luke Vander Vennen, Morgan Anderson, and Scott Moffatt, as well as Erin Mallon, from the lab of Dr. Merit Turetsky, at the University of Guelph, and Dr. Brent Patterson from the University of Trent, all of whom contributed to creating the forage and risk data sets integral to this project. Those same people were also always willing to explain the details involved in processing this massive data set, and were ever ready to help me develop and refine the concepts involved in this research.

I am grateful for personal financial support from Teaching Assistantships from the University of Guelph, from Research Assistantships and stipends from the University of Guelph

and to my advisor John Fryxell, and from the Ontario Graduate Scholarship program. Financial support for the wolf-caribou-moose demography project was provided by the Forest Ecosystem Science Co-operative Inc. NSERC CRD program, Canadian Forest Service, and the Wildlife Research and Development Division and the Center for Northern Forest Ecosystem Research of the Ontario Ministry of Natural Resources.

I owe much to every member of this extensive research team, and to all who funded this project. Their support helped turn this thesis into a reality.

TABLE OF CONTENTS

List of Tables.....	iv
List of Figures.....	iv
Introduction.....	1
Methods.....	3
Results.....	11
Discussion.....	13
Literature Cited.....	19
Tables and Figures.....	24

LIST OF TABLES

Table 1: The effect of resource and risk availability on seasonal-scale selection strength

LIST OF FIGURES

Figure 1: Study area map

Figure 2: Caribou selection strength for forage and avoidance of risk

Figure 3: Seasonal relationships between areas of high forage and high risk

Figure 4: Relationships between forage selection and risk avoidance

Figure 5: The effect of resource and risk availability on seasonal-scale selection strength

Figure 6: Step length and turn angle distributions

Figure 7: Relationships between seasonal (coarse) and local (fine) scales of selection

Figure 8: The effect of resource and risk availability on local-scale selection strength

INTRODUCTION

Natural landscapes are patchworks of varying forage abundance and risk. In such spatially heterogeneous landscapes, animals can selectively use some areas and avoid others in order to increase their chance of survival and reproduction (Gaillard et al. 2010). Examining habitat selection patterns relative to fitness variables is an important way to examine critical fitness constraints and to understand how individuals modify their behaviour to meet fitness challenges. Recent theory suggests that habitat selection strength should vary with habitat availability if there is a trade-off between two or more fitness variables (Myrsterud and Ims 1998). These predictions have thus far received limited attention, because few studies have appropriate data on fitness variables that span a wide range of availability.

Theory also suggests that animals may display different patterns of selection at different spatiotemporal scales (Orians and Wittenberger 1991). Little is currently known about the relationship between habitat selection patterns observed at fine scales compared to patterns observed at coarser temporal scales. On the one hand, fine-scale movement decisions and resource needs may create the selection patterns observed at broader scales, resulting in correlation between selection strengths at different scales (Owen-Smith et al. 2010). On the other hand, some studies have observed changes in selection strength at different spatial scales, possibly indicating that animals select for different resources at different scales (Rettie and Messier 2000). Careful consideration of functional responses in habitat selection at multiple spatial scales is thus necessary to gain a full understanding of habitat selection patterns relative to requirements for survival and reproduction (Gillies et al. 2006, Duchesne et al. 2010, Matthiopoulos et al. 2011).

Here I use space-use patterns of woodland caribou (*Rangifer tarandus caribou*) in the boreal forests of Northern Ontario to address five key questions. First, do caribou select for locations with high abundance of forage? Second, do caribou selectively use locations of low predation risk? Third, are there trade-offs between these two fitness variables across the landscape? Fourth, do caribou change the degree of selection for forage and avoidance of predation risk with changing levels of availability? Finally, do caribou change their habitat selection patterns at a fine spatial scale compared to that observed at the seasonal range scale.

Forage abundance and predation are thought to play large roles in caribou survival and reproduction. The diet of caribou consists primarily of lichen, supplemented in summer with forbs and graminoids (Rominger and Oldemeyer 1990, Rominger et al. 1996, Newmaster et al. 2013; Thompson et al. submitted MS). Wolves are the primary predators of caribou in many areas of their range (Seip et al. 1991, Bergerud et al. 1994, Festa-Bianchet et al. 2011). In several areas where caribou are threatened, there is evidence to suggest that increased predation by wolves has contributed to caribou declines (Seip 1992, Wittmer et al. 2005). Because forage abundance and wolf predation risk play roles in caribou survival and reproduction (Gustine et al. 2002), caribou should select forage and avoid risk on the landscape.

In this system, wolves primarily prey on moose, not caribou. In winter, when caribou diets (lichen) are very different from moose diets (forbs and shrubs), caribou are found far from moose. However, in summer, caribou diets include more forbs and graminoids, making their diet more similar to moose diets. Some authors suggest that this may bring caribou into closer

proximity with moose and consequently closer to wolves (Dussault et al. 2012). Caribou should not experience a forage-risk trade-off in winter, because their preferred winter forage species are located in areas away from moose forage species, and consequently farther from wolves. They should experience a forage-risk trade-off in the summer because their summer diet brings them closer in proximity to moose forage, and consequently, closer in proximity to wolves. Moreover, if forage, risk, and the trade-off between the two affect caribou space use, caribou should change selection strength in response to forage availability or risk prevalence in seasons in which they experience a forage-risk trade-off, but not in seasons in which they don't experience a forage-risk trade-off.

Finally, I compare seasonal-scale selection patterns with local (5 hour) selection patterns to see if caribou selection patterns are consistent across spatio-temporal scales. Because local selection decisions may generate the patterns seen at seasonal scales of selection (Owen-Smith et al. 2010), I expected caribou to have similar selection patterns at seasonal and local scales of selection. However, the alternative that caribou may select for different resources at different spatio-temporal scales (Rettie and Messier 2000) may create different selection patterns at seasonal and local selection scales.

METHODS

This study took place within a study area of 142,172 km² (defined by the range of caribou radio-telemetry fixes) in the boreal shield ecozone of northern Ontario, at latitudes ranging from 49°32' to 52°45'N and longitudes ranging from 84°27' to 93°23'W (Fig. 1). The area is largely characterized by rolling topography, lakes, bogs, fens, and coniferous and mixed-wood forests.

The dominant tree species in the area are white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*), intermixed with stands of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and balsam poplar (*Populus balsamifera*). This area spans a managed demarcation between southern forests in which commercial timber harvesting is allowed and more northerly forests in which commercial harvesting has not yet occurred (OMNR 2009). The animals in this study area face a broad gradient in ecological conditions. The southeastern, managed half of the landscape (located near the Nakina township) is characterized by younger forest stands more heavily dominated by mixedwood and deciduous tree species that have largely regenerated from anthropogenic disturbance, whereas the northwestern half of the study area (located near the Pickle Lake township) is characterized by older stands of coniferous species that have regenerated from natural disturbance, mainly windthrow or forest fires (OMNR 2009). The southeastern part of the study area has lower lichen density (Avgar et al. submitted MS), higher moose density (Street et al. submitted MS), higher wolf density (Kittle et al. submitted MS), and higher density of roads (LIO; <https://www.javacoeapp.lrc.gov.on.ca/geonetwork/srv/en/main.home>) than the un-harvested northwestern part of the study area. Together, the two parts of the study site expose caribou to a wide gradient of forage and risk conditions.

Landscape data for this study area were divided into a grid of hexagonal cells approximately 0.22 km² in area, whose centroids were separated by 500 m using ArcGIS software (ESRI 2014). Within each cell I assigned the distance (m) from the centroid of that cell to the nearest linear feature: paved roads, primary roads, secondary roads, and rail lines, from a

map provided by Land Information Ontario (LIO; <https://www.javacoeapp.lrc.gov.on.ca/geonetwork/srv/en/main.home>). Roads and cleared linear features are associated with both human vehicle traffic and wolf presence (Whittington et al. 2005). Including roads with high vehicle density in the model would attribute avoidance of these areas to road proximity (a proxy for vehicle traffic) rather than incorrectly attributing road avoidance to the effect of wolf presence and falsely inflating risk avoidance in this model. Those linear features used for human vehicle traffic (paved, primary, and secondary roads, as well as rail lines) were included as covariates in the RSF to account for the possibly confounding effect of vehicle avoidance on caribou habitat selection (Dyer and O'Neill 2002).

Individual cells were assigned a measure of digestible biomass (kg DM/m^2), weighted based on the composition of the caribou diet (Newmaster et al. 2013; Thompson et al. submitted MS, Avgar et al. submitted MS), and wolf density (wolves/ 100 km^2) for each season (i.e., summer and winter) and year (2010-2013). Winter was arbitrarily defined as November 1st through April 30th (approximating the period of snow cover) and summer as May 1st through October 31st.

To estimate dietary digestible biomass, the biomass of terrestrial lichen, shrubs, forbs, grasses, and mosses was measured in replicated 162 plots of 625cm^2 quadrats were sampled during the summer (Mallon 2014). Biomass values were converted to digestible biomass values using acid detergent fiber (ADF) and neutral detergent fiber (NDF) measurements for each plant category (terrestrial lichen, shrubs, forbs, grasses, and mosses) using plant samples taken from the region where possible, and supplemented with literature data otherwise (Mallon 2014).

Biomass values were then weighted based on the proportion of each plant class eaten by a caribou in either the winter or the summer (Newmaster et al. 2013, Thompson et al. submitted MS), resulting in season-specific models of dietary digestible biomass. These measurements of dietary digestible biomass were then fitted to the following land cover variables: Normalized Difference Vegetation Index (NDVI, a measure of greenness, obtained via the Land Processes Distributed Active Archive Center [LP DAAC 2014]) values, averaged over a season within a year (winter and summer for 2010, 2011, 2012, and 2013) and land cover type of the stand in which the measurement was taken using a log-linear model (Avgar et al. submitted MS). Land cover classes were based on the Ontario Provincial Far North Land Cover Database (FNLC v1.3.1; Ontario Ministry of Natural Resources 2013). The r^2 of these models (summer and winter for four years) ranged between 0.2 and 0.3. These models were then projected across the landscape to generate spatially explicit estimates of dietary digestible biomass for every cell in the landscape (Avgar et al. submitted MS).

Estimates of wolf density were based on a generalized least squares (GLS) landscape level model with explicit spatial correlation structure (Kittle et al., submitted MS). This model links the probability of wolf utilization, estimated using Brownian Bridge kernel density estimation (Horne et al. 2007) informed by wolf GPS data, to the following landscape variables: NDVI, FNLC land cover type (here, the percent water, lowland, deciduous, coniferous, mixed, sparse, and disturbed forest cover within a hexagonal cell on the landscape), garbage dump locations and settlement locations, distance to shore, and distance to nearest primary or paved road and distance to nearest secondary or tertiary road or rail or utility line. The r^2 of this model is 0.08. These probabilities were then multiplied by wolf pack size (estimated by aerial counts of

previously located packs), to convert them to localized wolf density (Kittle et al., submitted MS; i.e., per 0.22 km²). These values were then divided by the area of a pixel and multiplied by 100 to get a measurement of wolf density (wolves per 100 km²).

One hundred and ten adult female caribou, found opportunistically within the study site, were net-gunned from a helicopter and fitted with GPS telemetry collars (7000 MA and 7000 SW collars from Lotek Engineering, Newmarket, ON, Canada). Animal capture and handling followed Canadian Council on Animal Care Guidelines (CCAC 2003) and were approved annually by the Ontario Ministry of Natural Resources Animal Care Committee (protocols 10-, 11-, 12-183). GPS fixes were taken at 5-hour intervals for durations ranging from ten days to 3 years (36 months), depending on the length of the animal's collaring period. These data were taken between March 2010 and March 2013. Potentially erroneous GPS fixes (i.e., leading to unreasonable speeds or roundtrips) were removed. Further, I removed any GPS fixes that could not be used for both seasonal and local scale selection analyses. The local-scale step selection analysis (SSF; Fortin et al. 2005) using these location data (described below), required the calculation of a turn angle from a given starting point in order to generate a set of available points on the landscape. To calculate a turn angle, sequential GPS relocations are required. GPS technology occasionally fails to record a fix at the specified interval. I ensured that only GPS fixes that were preceded by two consecutive GPS fixes taken at approximately 5-hour fix intervals (4.5 - 5.5 hours), and during which a caribou were not stationary (moved more than zero meters), were used. To appropriately compare fine and seasonal scales of selection in other analyses, seasonal scale selection was also performed using this trimmed subset.

The data were divided by individual, by year, and by season. I kept only animal-season-year data sets that contained >50 GPS fixes to ensure a minimum time frame of approximately 10 days. I estimated the size of seasonal range for each individual by the 95% minimum convex polygon (MCP) fitted to the full set of fixes throughout one season using the `adehabitatHR` package in R (Calenge et al. 2006). I then kept only individual-season-years in which the densest 95% of the GPS fixes covered more than 10000 hectares. This ensured that there was enough variation in used and available data to generate selection coefficients for each animal in each season in each year. After removing data for animals with fewer than 50 GPS fixes or with seasonal ranges < 10000 ha, I were left with a final sample size of 100 individual-years for the summer season and 199 individual-years for the winter season. The number of fixes per caribou varied from 59 to 1149 with a mean of 482 fixes and the seasonal range area ranged from 10,030 ha to 394,200 ha with a mean of 65,400 ha.

To assess the degree of spatial trade-off between risk and forage faced by caribou on this landscape, I first calculated the correlation between the mean dietary digestible biomass across a seasonal range and mean wolf density within each individual's seasonal range. To assess the trade-off faced within seasonal ranges, I selected random points within each seasonal range and calculated Pearson's correlation between forage and risk for that random sample. The number of random points drawn within each seasonal range was set equal to the number of GPS fixes taken for the caribou in the time frame used to estimate its home range, ranging from 50 to 1100 random points per caribou per season.

To assess caribou selection for forage and avoidance of risk, I first assessed aggregate caribou space use behaviour. I calculated resource selection function (RSF) following a used-available design (Manly et al. 2002), pooling data from all caribou to estimate selection patterns shared by the entire population. I assumed GPS fixes to be used points and randomly drawn points within the seasonal ranges, as described above, as available points. I included animal identity, by season, by year as a random effect on the intercept to account for unbalanced sample sizes and to address spatial correlation (Breslow and Clayton 1993, Gillies et al. 2006). No within-group correlation structure was used. I fit these mixed-effect RSF models as functions of the form,

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n + \gamma_{0j}), \quad \text{Eq. 1}$$

where $w(x)$ is the relative probability of use, β_n is the estimated coefficient (strength of selection) for covariate x_n , and γ_{0j} is the random per-subject intercept for individual j . As explanatory variables, I included dietary digestible biomass, wolf density, and a binary variable representing distance to the nearest road. Based on a threshold in response to roads found by Latham et al. (2011) distances less than 1000 m were represented with 1 and distances greater than 1000 m with 0. I estimated population-level RSFs for both summer and winter to assess the population's general response to forage and risk on the landscape. I analyzed the seasons separately to account for seasonal differences in resource distribution and resource needs.

To evaluate the caribou functional response in resource selection, I estimated one RSF for each individual animal within a season within a year using the same explanatory variables as

described above. These coefficients, which calculated resource use relative to what was available within a seasonal range, represented seasonal-scale selection by individual caribou. I then regressed the selection coefficient for digestible biomass estimated by this function for each individual, within a season and year, against the availability of dietary digestible biomass in that animal's seasonal range. An identical procedure was used regress risk avoidance (negative one multiplied by the selection coefficient for risk, $\beta_{\text{wolf density}}$) estimated by each individual's RSF against the wolf density within its seasonal range. Separate regressions were calculated for each season. To examine the effect of trade-offs in risk and forage on selection patterns, I compared selection for forage with avoidance of risk using Pearson's correlation coefficient. A negative correlation here implies a trade-off between selection for forage and avoidance of risk.

To assess local scale selection patterns, I used an Step Selection Function (SSF; Fortin et al. 2005). An SSF compares the conditions across an observed GPS fix interval with conditions across theoretically available GPS fixes, presuming the focal animal started at the same start point. To create available relocations, I calculated empirical distributions of turn angles and net distances traveled between GPS fixes (step lengths), splitting data between seasons, but pooling data from all caribou. For every GPS fix in the analysis, I then generated 10 alternative, available, relocation points using randomly-drawn turn angles and distances from the empirical distribution for the appropriate season.

As before, I partitioned the data by caribou, by season, and by year. For each unique animal and time frame, I then ran a case-control logistic regression (for details see Fortin et al. 2005) to estimate selection. I used the same three variables as in the coarse-scale analysis, with

one modification. To describe distance to nearest road, I used the distance (m), rather than a binary variable. Using a binary variable for proximity to road did not provide enough variability for the SSF model to converge, an error corrected by using a continuous variable.

To understand the relationship between seasonal and local scales of selection, I compared the coefficients of selection for forage and avoidance of risk estimated by the SFF to those estimated by the coarse-scale analysis using linear regression, with local scale (SSF) selection strength as the predictor variable. Finally, I examined the influence of availability on fine-scale selection strength by regressing the SSF selection coefficients against the available digestible biomass and average wolf density within each seasonal range, as previously done for the coarse analysis coefficients.

RESULTS

Caribou selected for habitats high in dietary digestible biomass, avoided areas of high wolf density, and avoided areas near roads in both the summer and the winter (Fig. 2) indicating that forage and risk do play a role in shaping caribou space use. Caribou experienced a wide range of conditions on this landscape. In the summer, average digestible biomass values within seasonal ranges ranged from 0.014 to 0.037 kg DM/m² and average wolf density values within seasonal ranges ranged from 0.205 to 0.286 wolves/100 km². In the winter, digestible biomass values ranged from 0.022 to 0.063 kg DM/m² and relative wolf density values ranged from 0.200 to 0.295 wolves/100 km². Caribou faced a spatial trade-off between high-forage and low-risk locations during summer, as indicated by a positive correlation between mean values of wolf density and forage availability within each caribou seasonal range ($r = 0.315$, $P < 0.001$, $df = 112$

; Fig. 3). They also face a correlation between forage and risk at locations within summer ranges ($r = 0.193$, $P < 0.001$, $df = 63823$). This relationship was reversed in the winter, both when comparing across caribou seasonal ranges ($r = -0.473$, $P < 0.001$, $df = 208$; Fig. 3) and at locations within winter ranges ($r = -0.332$, $P < 0.001$, $df = 77843$). In contrast to these patterns, coefficients of selection for forage and avoidance of risk by woodland caribou were negatively correlated during winter ($r = -0.180$, $P = 0.011$; Fig. 4), but not during summer ($r = -0.039$, $P = 0.703$; Fig. 4).

At seasonal scales of selection, variation across individuals in the avoidance of risk was consistently influenced by the degree of risk across the landscape (Fig. 5), both in winter (Table 1) and summer (Table 1). Specifically, risk avoidance was higher in riskier seasonal ranges. Individual caribou decreased their selection for dietary digestible biomass when food was more abundant within their seasonal range during winter (Table 1), but not summer (Table 1).

The distribution of 5h step lengths, used to generate available fixes for the fine-scale selection analysis, was heavy-tailed. Caribou most frequently moved < 500 m within 5-hour intervals, but they occasionally covered much larger distances (Fig. 6a). The farthest a caribou traveled in 5 hours during the summer was 24.8 km and the farthest a caribou traveled in the winter was 35.3 km. Caribou had a roughly uniform distribution of turn angles (Fig. 6b).

Patterns of habitat selection observed at fine spatial scales largely mirrored those observed at the seasonal scale. Seasonal and local scale selection coefficients were positively correlated in both seasons and for both fitness measures (forage and risk; Fig. 7). In winter, local

scale (SSF) selection for forage decreased with increased forage availability ($\beta = -347.7$, $P < 0.001$, $r^2 = 0.12$) and avoidance of risk increased with increased wolf density ($\beta = 107.4$, $P < 0.001$, $r^2 = 0.08$). In summer, on the other hand, selection for forage was insensitive to changes in forage availability ($\beta = -445.4$, $P = 0.192$, $r^2 < 0.01$) whereas avoidance of risk still increased with increased wolf density ($\beta = 96.0$, $P = 0.012$, $r^2 = 0.05$; Fig. 8). This pattern is similar to the pattern observed at a seasonal scale. Like at seasonal scales, there was little apparent correlation between step selection coefficients for risk avoidance and forage among individuals in summer at local scales ($r = 0.127$, $P = 0.073$, $df = 197$) but there was a negative correlation between selection for forage and avoidance of risk in winter ($r = -0.180$, $P = 0.007$, $df = 222$).

DISCUSSION

This study differs from most other resource selection studies by evaluating selection of habitats in direct relation to fitness-related metrics (food availability and predation risk) rather than broad landscape categories, allowing direct assessment of the relative importance of fitness-related metrics to individuals in different locations and in different seasons (Aarts et al. 2013). Unlike the results of studies comparing space use to broad landscape categories, my results directly demonstrate that woodland caribou select habitats with higher food availability and lower wolf density, even after accounting for caribou's avoidance of roads, at both seasonal and local spatial scales. Hence both fitness-related metrics were important in guiding patterns of caribou space use. There is a difference in selection strength between summer and winter (Fig. 2). However, barring further analysis, it is difficult to determine whether that difference reflects an actual change in preference (Johnson 1980) or a change in resource availability between the two seasons.

Forage-Risk Trade-offs, Availability, and Selection

The observed seasonal shift in the forage-risk correlation on the landscape may be related to a seasonal shift in caribou diet. In the boreal forest, ground lichens that form the bulk of caribou diets during winter are found primarily in stands of mature coniferous forest. In these forest types there is little forage for moose, and consequently, these areas are rarely frequented by moose or wolves (Cumming et al. 1996, Kittle et al. submitted MS, Street et al. submitted MS). In the summer, caribou expand their diet to include a wide variety of forbs and graminoids that thrive in more productive, early seral stands (Newmaster et al. 2013; Thompson et al. submitted MS). Perhaps as a result of this diet shift, caribou forage in stands that typically have higher population densities of both wolves and moose (Dussault et al. 2012), resulting in the observed forage-safety tradeoff in summer, despite the lack thereof in winter.

A functional response in habitat selection implies either that increased use of a resource comes at a cost (Myerud and Ims 1998) or that there are diminishing returns to habitat selection when preferred habitats are readily available (Aarts et al. 2013). If such constraints are not in place, it is hard to imagine why an animal would not simply increase resource use with increasing habitat availability across the landscape, thus maintaining a constant strength of habitat selection. Woodland caribou in my study areas did not consistently face a trade-off between predation risk and food abundance. In winter, safe sites also provided the most food. In summer, however, there was a change in spatial correlation (i.e., from negative to positive) between forage availability and predation risk, such that caribou could only maximize safety by choosing sites with lower than average food abundance. Hence, according to the hypothesis that

trade-offs drive functional responses in habitat selection (Mysterud and Ims 1998), functional responses should have occurred in summer, but not winter. That a functional response with respect to predation risk occurred in both seasons and a functional response with respect to food abundance occurred in the winter but not summer suggests that other trade-offs come into play or that there are diminishing returns to selecting for food availability during certain periods of the year. Mabile et al. (2012) similarly failed to find a consistent correlation between selection for cover from predation and selection for forage by moose, even in landscapes where forage and risk were positively correlated.

Scales of Selection

Selection for forage and avoidance of risk at seasonal and local scales were correlated, suggesting that caribou responded to availability in qualitatively the same way at both spatio-temporal scales. Ecologists aim to both understand fine-scale behaviours using relatively seasonal scale data and to predict population persistence or create effective long-term management strategies (i.e., predict coarse-scale patterns) using relatively fine-scale landscape or behavioural data (Gaillard et al. 2010, Morales et al. 2010, Owen-Smith et al. 2010). To do either, it is imperative to understand the relationship between patterns observed at multiple scales.

There are many possible interpretations of the correlation between seasonal and local scales of caribou habitat selection. The first views habitat selection as a result of foraging decisions. Space-use decisions made by individuals may scale up to create selection patterns observed at both scales of selection observed in this study (Owen-Smith et al. 2010), provided

that both scales of selection reflect the same behavioural mode and decision-making framework (i.e., foraging rather than searching; Getz and Saltz 2008) or the same ecological domain (Wiens 1989).

The second interpretation starts from the premise that selection at different spatio-temporal scales may operate independently of one-another (Orians and Wittenberger 1991). If this is true, selection processes at different scales will be nested hierarchically (Johnson 1980) and selection at fine scales should be constrained by the results of selection processes operating at coarser scales (Rettie and Messier 2000). When coarse scale selection for the most limiting resource significantly increases the fine scale availability of that resource, selection for that resource at a fine scale should be low, but if coarse scale selection for the most limiting resource does not significantly increase availability at a fine scale, then selection indices should be similar across scales. According to this logical framework, the similarity between local and seasonal selection for woodland caribou in my study results not from selection being within the same domain, but independent selection at both scales driven by similar resource requirements (Hins et al. 2009). Moreover, if the environmental conditions experienced or available at one scale are correlated with those at another, then patterns observed at one scale would necessarily be correlated to patterns observed at another, regardless of underlying mechanism or framework (Battin and Lawler 2006, Lawler and Edwards 2006).

Landscape Projections of Fitness Variables in Habitat Selection Studies

Use of explicit resource variables allowed us to explicitly examine forage-risk correlations on the landscape, and to directly assess and interpret selection for resources. While I

believe that this approach is advantageous, there are also challenges in taking a resource-oriented approach to habitat selection. To do so over a large geographical range, one must rely on complex predictive models of resource distribution that are applicable over a large spatial domain; models that generally perform poorly (Barry and Elith 2006). Often multiple factors that play a role in determining distribution and density of plants or animals (from cover type and stand age to elevation, precipitation, and temperature), and their effects can be mediated by temporal changes (Polansky and Wittemyer 2011) and by landscape configuration (Shreeve and Dennis 2010). The error associated with measurements of explanatory variables accumulates as they are incorporated into modeling frameworks (Barry and Elith 2006). However, these problems also occur when using crude land cover variables, such as NDVI or land cover type. By characterizing spatial variation in both food abundance and predation risk, researchers should be better poised to relate habitat selection more clearly to factors that govern fitness and reproduction, even though I acknowledge the uncertainty inherent in this methodological approach.

Though spatially-explicit measures of food abundance and predation risk may represent an improvement over crude habitat classes, these metrics are still one step removed from true fitness variables. Digestible biomass may not be the primary factor limiting growth and reproduction in caribou (Bergman et al. 2001, Hebblewhite et al. 2008). Moreover, some authors have pointed out that predator density is not the only determinant of predation risk – several factors work together to determine the actual probability of death (Hebblewhite et al. 2005). Significant challenges remain in extrapolating true fitness variables from landscape variation in food abundance and predator density.

Management Implications

Habitat selection studies have been used to define ranges (Johnson and Seip 2008) and identify critical habitats (Nielsen et al. 2006) pursuant to conservation or management goals. However, anthropogenic disturbance often generates landscape change at a rapid pace, and alters the availability of resources on the landscape. Knowing how habitat selection changes in response to changes in availability is thus key to understanding observed shifts in critical habitats in pristine and disturbed landscapes (Osco et al. 2004, Sawyer et al. 2006). Moreover, the relationship between selection at multiple spatial scales is still poorly understood (Mayor et al. 2009). Due to the large spatial scale over which anthropogenic disturbance operates, caribou may not shift home ranges away from disturbed areas (Hins et al. 2009). Thus, selection for forage-rich and safe areas at finer scales (e.g. within the disturbed landscape) could play a crucial role in caribou survival. Understanding how populations of caribou respond to human-driven landscape changes across multiple spatial scales could therefore be important for caribou conservation and management.

LITERATURE CITED

- Aarts, G., J. Fieberg, S. Brasseur, and J. Matthiopoulos. 2013. Quantifying the effect of habitat availability on species distributions. *The Journal of animal ecology* 82:1135–45.
- Avgar, T., J. A. Baker, G. S. Brown, J. Hagens, A. M. Kittle, E. E. Mallon, M. T. McGreer, A. Mosser, S. G. Newmaster, B. R. Patterson, D. E. B. Reid, A. R. Rodgers, J. Shuter, G. M. Street, I. D. Thompson, M. Turetsky, P. A. Wiebe, and J. M. Fryxell. Submitted MS. Space-use behaviour of woodland caribou based on a cognitive movement model. *Journal of Animal Ecology*.
- Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* 43:413–423.
- Battin, J., and J. Lawler. 2006. Cross-scale correlations and the design and analysis of avian habitat selection studies. *The Condor* 108:59–70.
- Van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84:723–735.
- Bergerud, A. T., I. Road, S. Island, and V. K. Canada. 1994. Evolving perspectives on caribou population dynamics, have I got it right yet? *Rangifer*:95–115.
- Bergman, C. M., J. M. Fryxell, C. C. Gates, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology* 70:289–300.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.
- Brown, J. S. 1999. Vigilance , patch use and habitat selection : Foraging under predation risk:49–71.
- Canadian Council on Animal Care (CCAC). 2003. Guidelines on the care and use of wildlife. CCAC, Ottawa, ON, Canada.
<<http://www.ccac.ca/Documents/Standards/Guidelines/Wildlife.pdf>>
- Cumming, H. G., D. B. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer*:81–94.
- Duchesne, T., D. Fortin, N. Courbin, and D. Mathe. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79:548–555.
- Dussault, C., V. Pinard, J.-P. Ouellet, R. Courtois, and D. Fortin. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 279:4481–8.

- Dyer, S., and J. O'Neill. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80:839–845.
- Dzus, E. 2001. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta. Page 47. Edmonton, AB.
- ESRI 2014. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Cote, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- Fortin, D., H. L. H. Beyer, M. M. S. Boyce, D. W. D. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2255–2265.
- Getz, W. M., and D. Saltz. 2008. A framework for generating and analyzing movement paths on ecological landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 105:19066–71.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165:1–32.
- Hansen, B. B., I. Herfindal, R. Aanes, B.-E. Saether, and S. Henriksen. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos* 118:859–872.
- Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834–844.
- Hebblewhite, M., E. H. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* 111:101–111.

- Hins, C., J.-P. Ouellet, C. Dussault, and M.-H. St-Laurent. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. *Forest Ecology and Management* 257:636–643.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–63.
- Johnson, C. J., and D. R. Seip. 2008. Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. *Population Ecology* 50:145–157.
- Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kittle, A. M., B. R. Patterson, M. Anderson, S. Moffatt, A. R. Rodgers, J. Shuter, D. E. B. Reid, J. A. Baker, G. S. Brown, I. D. Thompson, G. M. Street, T. Avgar, L. M. Vander Vennen, A. Mosser, J. Hagens, E. Iwachewski, and J. M. Fryxell. Submitted MS. Wolves adapt territory size, not pack size to local habitat quality. *Journal of Animal Ecology*.
- Latham, A., M. Latham, M. S. Boyce, and S. Boutin. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications* 21:2854–2865.
- Lawler, J., and T. C. Edwards. 2006. A variance-decomposition approach to investigating multiscale habitat associations. *The Condor* 108:47–58.
- Mabille, G., C. Dussault, J. Ouellet, and C. Laurian. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. *Oecologia* 170:965–977.
- Mallon, E. E. 2014. Effects of Disturbance and Landscape Position on Vegetation Structure and Productivity in Ontario Boreal Forests : Implications for woodland caribou (*Rangifer tarandus caribou*) Forage. Thesis, University of Guelph.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Second Edi. Kluwer Academic, Dordrecht.
- Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalized functional responses for species distributions. *Ecology* 92:583–589.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat Selection at Multiple Scales. *Ecoscience* 16:238–247.
- Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2289–301.

- Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441.
- NASA Land Processes Distributed Active Archive Center (LP DAAC). ASTER L1B. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota. 2001 .
- Newmaster, S. G., I. D. Thompson, R. A. Steeves, A. R. Rodgers, A. J. Fazekas, J. R. Maloles, R. T. McMullin, and J. M. Fryxell. 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. *Canadian Journal of Forest Research* 43:897–900.
- Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130:217–229.
- OMNR. November 2009. Forest Management Planning Manual for Ontario’s Crown Forests. Toronto: Queen’s Printer for Ontario. 447 pp. Ontario Ministry of Natural Resources. 2013. Far North Land Cover Data Specifications (Version 1.3). Page 30 pp. Ontario Ministry of Natural Resources.
- Orians, G., and J. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.
- Osko, T. J., M. N. Hiltz, R. J. Hudson, and S. M. Wasel. 2004. Moose habitat preferences in response to changing availability. *Journal of Wildlife Management* 68:576–584.
- Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2267–2278.
- Polansky, L., and G. Wittemyer. 2011. A framework for understanding the architecture of collective movements using pairwise analyses of animal movement data. *Journal of the Royal Society: Interface* 8:322–33.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- Rominger, E. M., and J. L. Oldemeyer. 1990. Early-winter diet of woodland caribou in relation to snow accumulation, Selkirk Mountains, British Columbia, Canada. *Canadian Journal of Zoology* 68:2691–2694.
- Rominger, E. M., C. T. Robbins, and M. A. Evans. 1996. Winter foraging ecology of woodland caribou in Northeastern Washington. *Journal of Wildlife Management* 60:719–728.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.

- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494–1503.
- Seip, D. R., B. C. M. Forests, C. Way, B. C. Canada, and S. Georgia. 1991. Predation and caribou populations. *Rangifer*:46–52.
- Shreeve, T. G., and R. L. H. Dennis. 2010. Landscape scale conservation: resources, behaviour, the matrix and opportunities. *Journal of Insect Conservation* 15:179–188.
- Street, G. M., A. R. Rodgers, and J. M. Fryxell. Submitted MS. Seasonality and temperature variation influence habitat selection by moose. *Journal of Wildlife Management*.
- Whittington, J., C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15:543–553.
- Wiens, J. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144:257–67.

TABLES AND FIGURES

Table 1.

The estimated relationships (coefficients from linear regression) between selection for biomass and available digestible biomass (kg DM/ m²) in the seasonal range and the estimated relationships avoidance of predation risk and average wolf density (wolves/100 km²) within the seasonal range the summer and in the winter.

		coefficient	p-value	r ²
Summer	Effect of available biomass on selection for biomass	2470.1	0.129	0.01
	Effect of average wolf density on avoidance of predation risk	378.4	0.001	0.09
Winter	Effect of available biomass on selection for biomass	-820.9	< 0.001	0.14
	Effect of average wolf density on avoidance of predation risk	356.1	< 0.001	0.16

Figure 1.

On the left, a map of the study site (grey) relative to Ontario's borders and the Area of Undertaking (hash pattern), in which forestry is currently permitted. On the right, the inset shows maps of wolf risk (top) and dietary digestible biomass (bottom) in the summer of 2010.

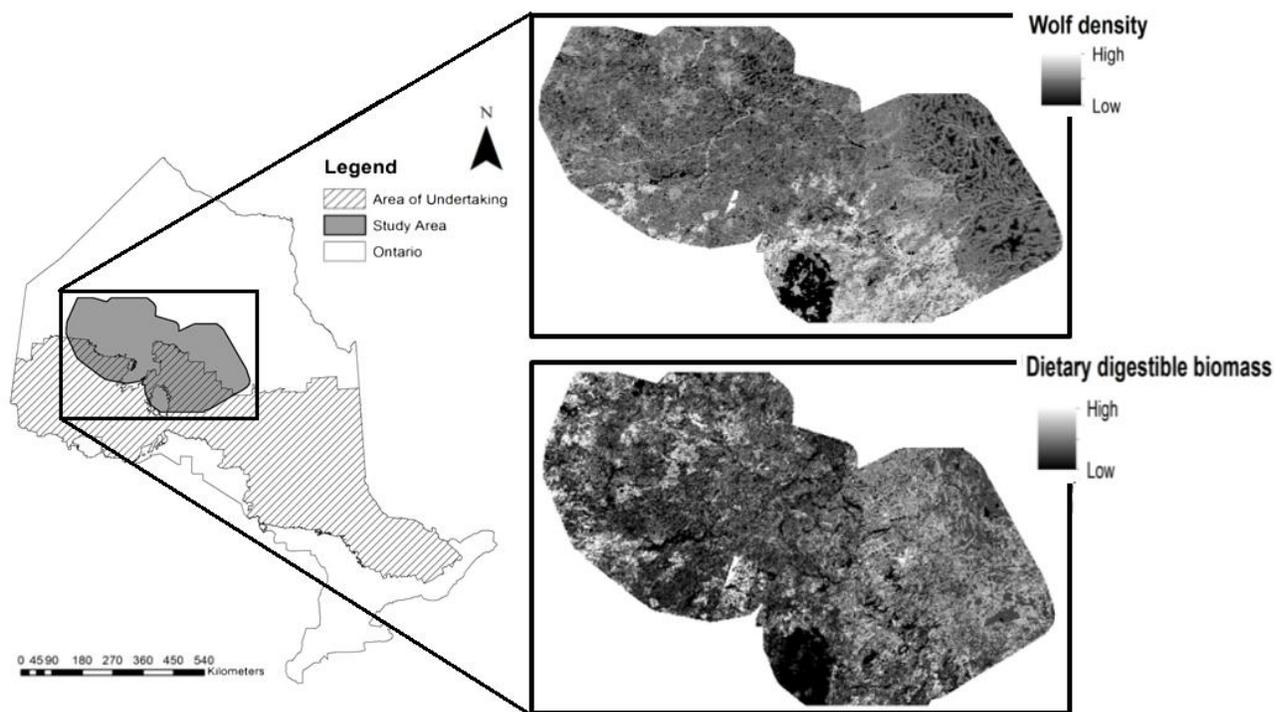


Figure 2.

Population-level selection coefficients for digestible biomass, avoidance of predation risk, and selection for distance away from the nearest road. The bars represent the 95% confidence intervals around the selection coefficients. The random intercept in winter has a standard deviation of 0.3037 and the random intercept in summer has a standard deviation of 0.415 in winter.

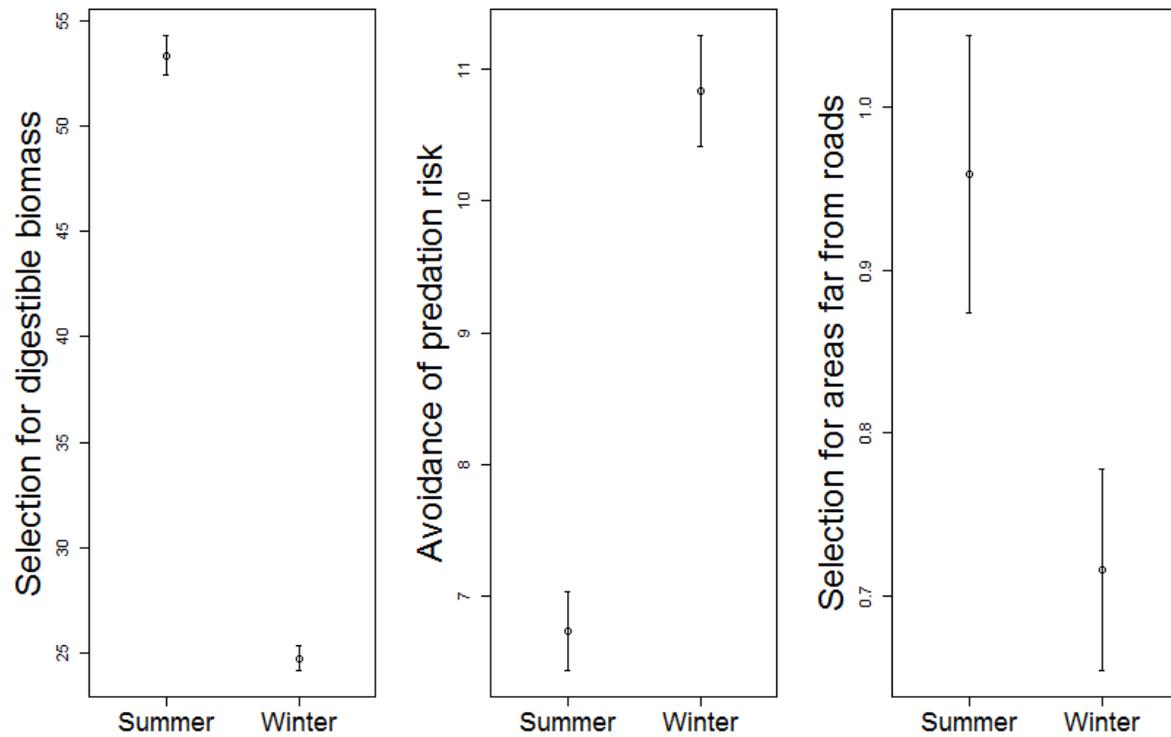


Figure 3.

The relationship between available digestible biomass ($\text{kg DM}/\text{m}^2$) and average wolf density ($\text{wolves}/100 \text{ km}^2$) within seasonal ranges. Lines represent significant relationships.

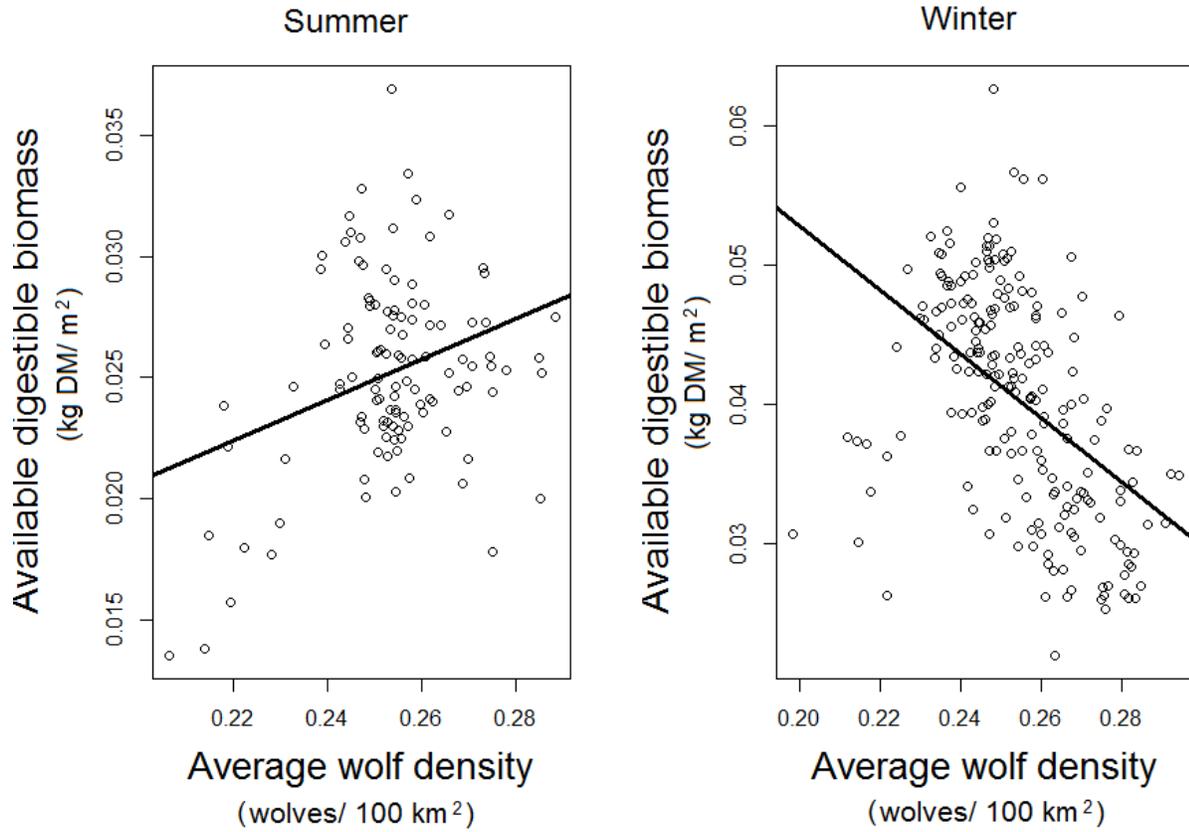


Figure 4.

The relationship between selection for forage and risk avoidance at seasonal scales (left panels; coarse scales) and local scales (right panels; fine scales) of selection in both the summer (top panels) and winter (bottom panels). The line represents a significant relationship (top left: $\beta = -0.106$, $P = 0.184$, $r^2 = 0.008$, bottom left: $\beta = -0.047$, $P = 0.011$, $r^2 = 0.028$, top right: $\beta = -0.009$, $P = 0.703$, $r^2 = -0.004$, bottom right: $\beta = -0.028$, $P = 0.076$, $r^2 = 0.009$)

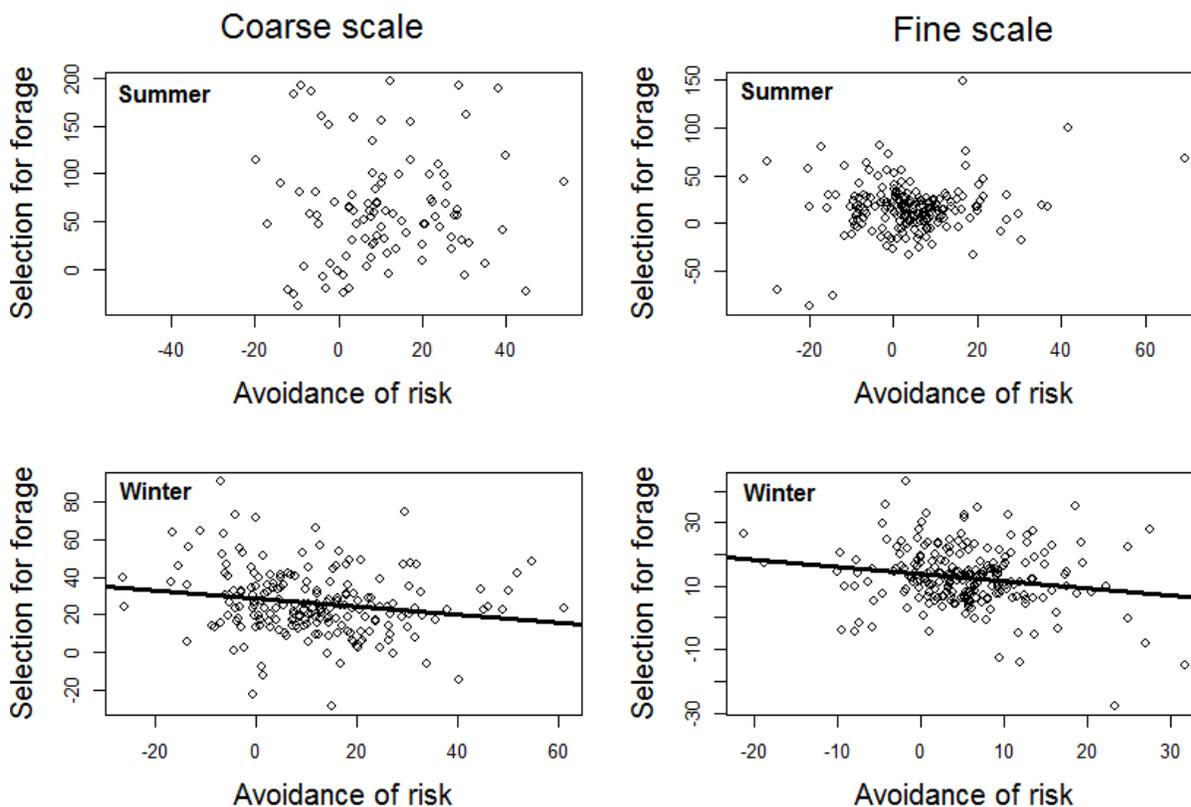


Figure 5.

Seasonal scale selection for biomass (top) and seasonal scale avoidance of predation risk (bottom) as a function of available digestible biomass ($\text{kg DM}/\text{m}^2$) and average wolf density (wolves/ 100 km^2) respectively, shown for both the summer and in the winter. Lines indicate significant regression slopes.

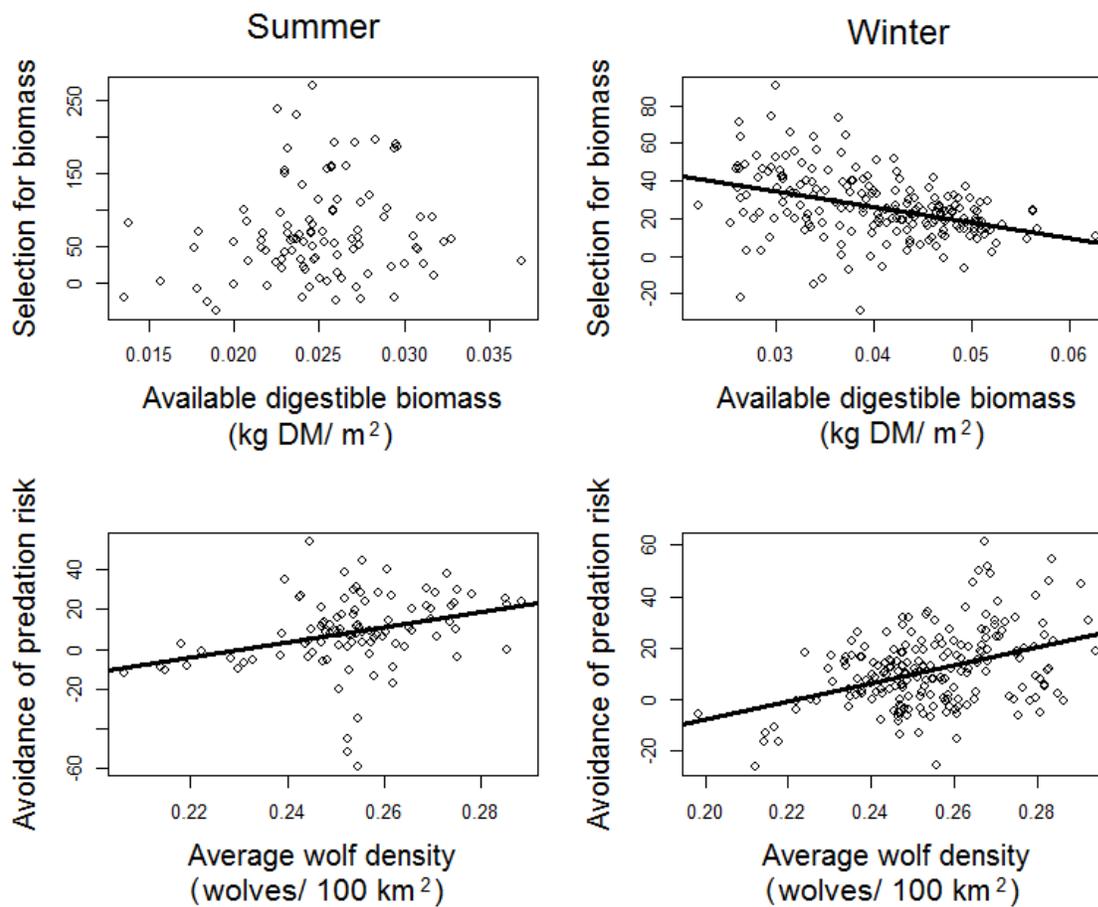
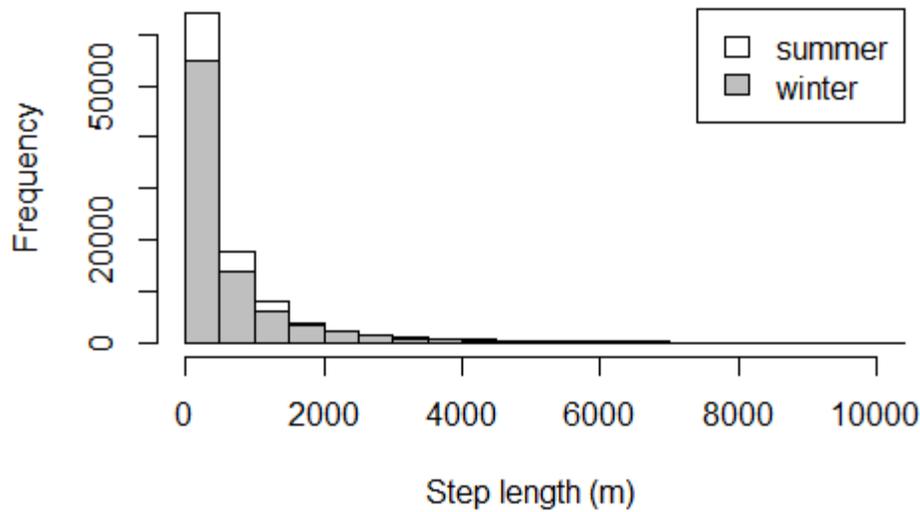


Figure 6.

Summer (white) and winter (grey) distributions of net distance traveled (a), in meters and turn angle distributions (b), in degrees. The median step length is 299.3 m in summer and 301.1 m in winter. The histogram of step length does not show bins with 50 or fewer steps in both distributions. Bins are in increments of 500 m.

a)



b)

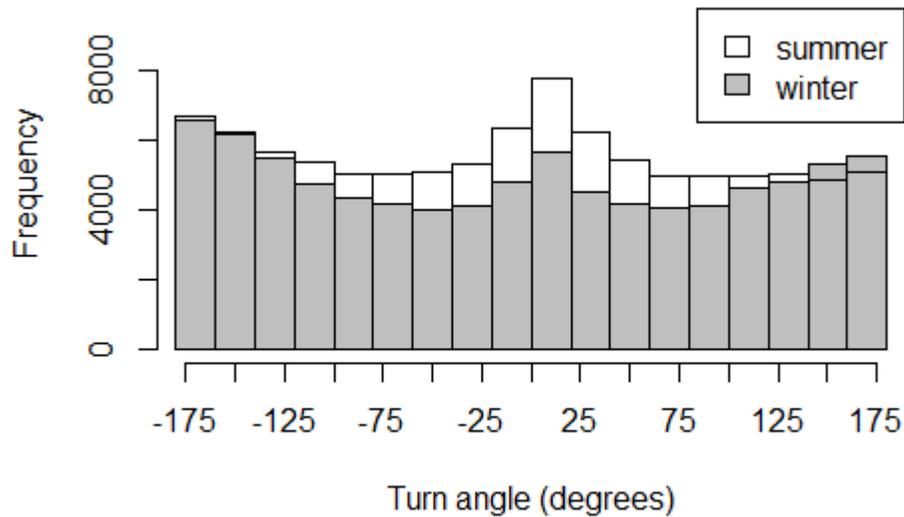


Figure 7.

The relationship between seasonal scale (coarse scale) and local scale (fine scale) selection for forage (top) and avoidance of risk (bottom) in the summer (circles) and the winter (triangles). Lines indicate significant regression slopes for the summer (short dashes; $\beta = 0.105$, $P < 0.001$, $r^2 = 0.193$ for biomass selection and $\beta = 0.163$, $P < 0.001$, $r^2 = 0.265$ for risk avoidance) and winter (long dashes; $\beta = 0.308$, $P < 0.001$, $r^2 = 0.365$ for biomass selection and $\beta = 0.320$, $P < 0.001$, $r^2 = 0.528$ for risk avoidance).

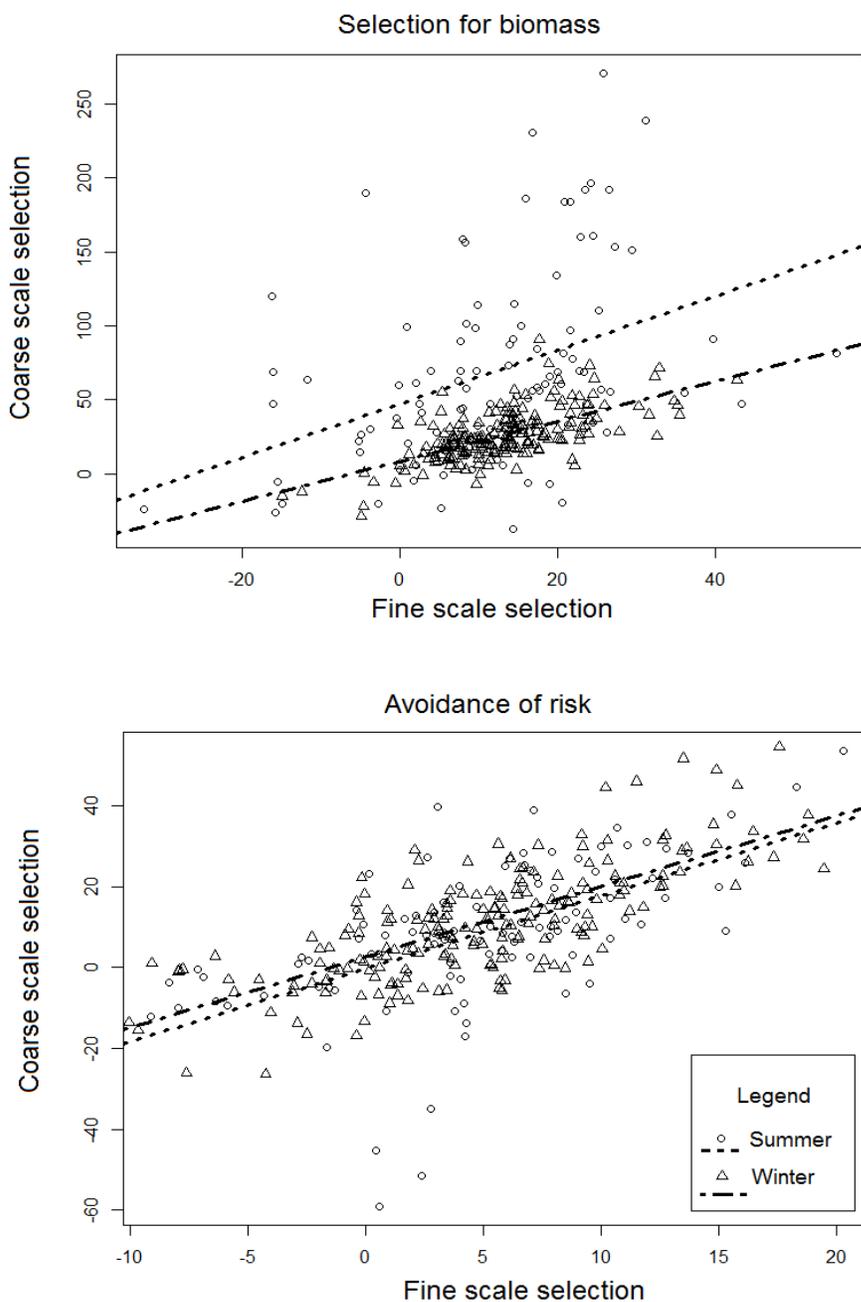


Figure 8.

Local scale (fine scale) selection for biomass (top) and local scale (fine scale) avoidance of predation risk (bottom) as a function of available digestible biomass (kg DM/m²) and average wolf density (wolves/100 km²) respectively, shown for both the summer and in the winter. Lines indicate significant slopes (response of forage selection to availability in summer: $\beta = -445.4$, $P = 0.192$, $r^2 = 0.007$, response of risk avoidance to availability in summer: $\beta = 1984.2$, $P = 0.012$, $r^2 = 0.053$, response of forage selection to availability in winter: $\beta = -347.7$, $P < 0.001$, $r^2 = 0.110$, response of risk avoidance to availability in winter: $\beta = 2218.2$, $P < 0.001$, $r^2 = 0.077$).

