Selection for forage and avoidance of risk by woodland caribou (*Rangifer tarandus caribou*) at coarse and local scales

Madeleine T. McGreer,[1,†] Erin E. Mallon,[1] Lucas M. Vander Vennen,[1,2] Philip A. Wiebe,[3] James A. Baker,[4] Glen S. Brown,[5] Tal Avgar,[1,6] Jevon Hagens,[4] Andrew M. Kittle,[1] Anna Mosser,[1,5] Garrett M. Street,[1] Doug E. B. Reid,[4] Arthur R. Rodgers,[4] Jennifer Shuter,[4] Ian D. Thompson,[4] Merritt J. Turetsky,[1] Steven G. Newmaster,[1] Brent R. Patterson,[2] and John M. Fryxell[1]

[1]*Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1 Canada*
[2]*Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, 300 Water Street, Peterborough, Ontario K9J 3H2 Canada*
[3]*Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, Ontario P6A 2E5 Canada*
[4]*Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research 435 South James Street, Suite B001, Thunder Bay, Ontario P7E 6S8 Canada*
[5]*Ontario Ministry of Natural Resources and Forestry, Ontario Wildlife Population Monitoring Program, 1235 Queen Street East, Sault Ste. Marie, Ontario P6A 2E5 Canada*

Abstract.   The relationship between selection at coarse and fine spatiotemporal spatial scales is still poorly understood. Some authors claim that, to accommodate different needs at different scales, individuals should have contrasting selection patterns at different scales of selection, while others claim that coarse scale selection patterns should reflect fine scale selection decisions. Here we examine site selection by 110 woodland caribou equipped with GPS radio-collars with respect to forage availability and predation risk across a broad gradient in availability of both variables in boreal forests of Northern Ontario. We tested whether caribou selection for forage and avoidance of risk was consistent between coarse (seasonal home range) and fine scales of selection. We found that local selection patterns predicted coarse scale selection patterns, indicating a close relationship between the drivers of selection at both spatial scales.

[6] Present address: Department of Biological Sciences, University of Alberta, 116 Street and 85 Avenue, Edmonton, Alberta T6G 2R3 Canada.
[7] Present address: College of Biological Sciences, University of Minnesota Twin Cities, 1445 Gortner Avenue, St Paul, Minnesota 55108 USA.
† E-mail: mcgreerm@uoguelph.ca

Introduction

Natural landscapes are often patchworks of varying habitat types. In such spatially hetero-geneous landscapes, animals selectively use some areas and avoid others, presumably to increase their chance of survival and reproduction (Gaillard et al. 2010). Little is currently

known about the relationship between habitat selection patterns observed at fine scales compared to patterns observed at coarser temporal scales. Fine-scale movement decisions and resource needs might give rise to the selection patterns observed at broader scales, a process we term the scaling-up hypothesis, resulting in correlation between selection strengths at different scales (Levin 1992, Owen-Smith et al. 2010). On the other hand, both theory and a limited set of observations suggest that some species display different patterns of selection at different spatiotemporal scales (Orians and Wittenberger 1991, Rettie and Messier 2000), possibly indicating which factors are most limiting to population growth (Rettie and Messier 2000). As a result, resource selection patterns would form a hierarchy that would match ecological limiting factors, a process we term the scale-dependent fitness hypothesis.

Careful consideration of 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 (Matthiopoulos et al. 2011). Here we use space-use patterns of woodland caribou (*Rangifer tarandus caribou*) in the boreal forests of Northern Ontario to address this question: do woodland caribou change their habitat selection patterns at a fine spatial scale compared to that observed at the seasonal home range scale?

Caribou diet consists primarily of lichen, supplemented in summer with forbs and graminoids (Rominger and Oldemeyer 1990, Newmaster et al. 2013, Thompson et al. 2015). These foods vary widely across different forest stand types in the boreal zone (Mallon 2014). Accordingly, one might expect woodland caribou to concentrate their activity in forest stands that best supply the foods that caribou prefer. Despite the fact that moose (*Alces alces*) predominate in their diet, wolves (*Canis lupus*) nonetheless often have a strong impact on woodland caribou populations (Seip et al. 1991, Bergerud et al. 1994, Festa-Bianchet et al. 2011). Wolves tend to spend most of their time in early successional forests, presumably because these are the habitats preferred by moose, their primary prey (Cumming et al. 1996, Kittle et al. 2015). Because forage abundance and wolf predation risk play important roles in caribou survival and repro-

duction (Gustine et al. 2006), caribou have a clear opportunity to select habitats that improve fitness either through increased access to forage or reduced risk of predation as caribou move across heterogeneous boreal landscapes.

Here we compare seasonal-scale habitat selection patterns of individual woodland caribou at the seasonal home range scale with their local habitat selection patterns at the daily movement scale. If statistical measurements of behavioral tendencies at any spatiotemporal scale are simple summations of the decisions made over shorter timeframes and smaller spatial arenas (Levin 1992, Owen-Smith et al. 2010), then the scaling-up hypothesis predicts that selection strengths of individual caribou should be positively correlated at coarse and fine scales of selection. On the other hand, if the impact of predation risk and energy gain on caribou vital rates differ in magnitude at different spatiotemporal scales (Rettie and Messier 2000), then the scale-dependent fitness hypothesis predicts one might expect the most limiting factor to dominate resource selection at the coarser spatiotemporal scale and a neutral or even inverse relationship between selection coefficients for predation risk and food availability measured at coarse vs. fine spatiotemporal scales (Rettie and Messier 2000).

Methods

This study took place within a study area of 142,172 km^2 (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. The managed half of the landscape (located near
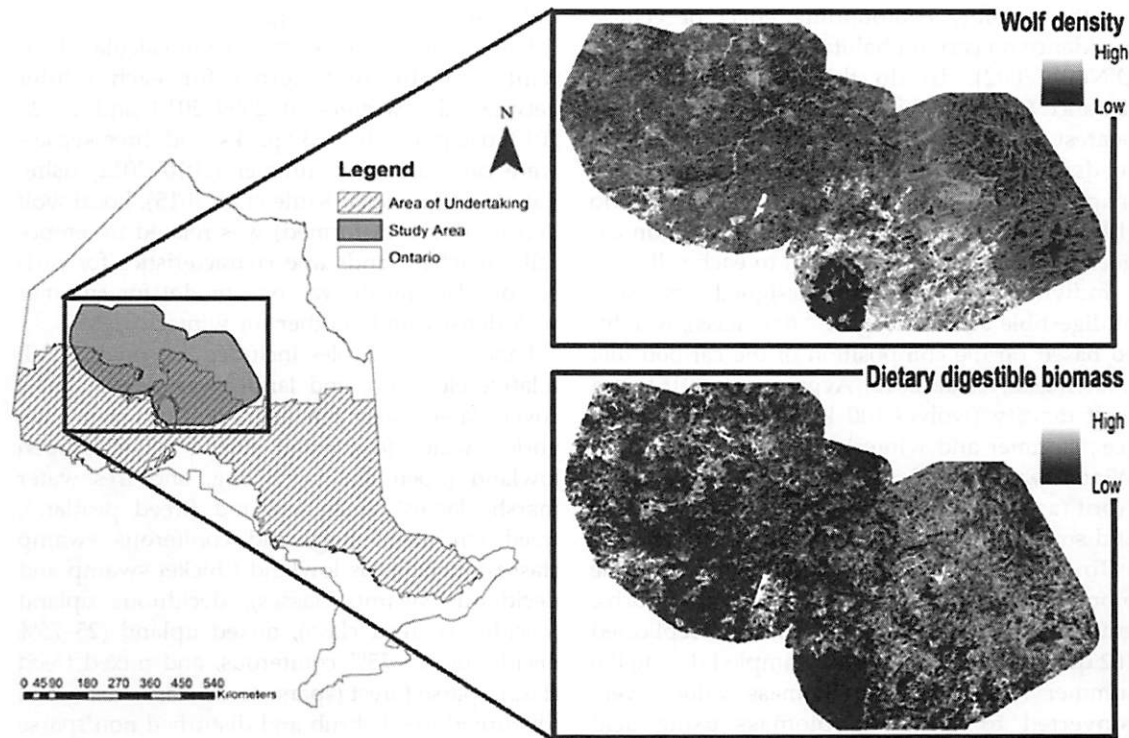
Fig. 1. A map of the study site (grey) relative to Ontario's borders and the Area of Undertaking (hash pattern), in which forestry is currently permitted. The inset shows maps of our study area depicting spatial variation in wolf density (top) and dietary digestible biomass (bottom) in the summer of 2010.

the Nakina township) is characterized by younger forest stands dominated by mixedwood and deciduous 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. The southeastern part of the study area has lower lichen density (Avgar et al. 2015), but higher densities of both moose and wolves (Kittle et al. 2015, Street et al. 2015). Because of extensive logging activity, the southeastern part of the study also has higher road density (LIO; https://www.javacoeapp.lrc. gov.on.ca/geonetwork/srv/en/main.home) than the un-harvested northwestern part of the study area. Because of their different management histories, the two parts of the study site expose caribou to a wide gradient of forage and risk conditions.

Landscape data were divided into a grid of hexagonal cells approximately 0.22 km^2 in area, with centroids separated by 500 m, using ArcGIS software (ESRI 2014). Hexagonal cells are preferable to a square grid because, in a hexagonal grid, each cell has six equidistant adjacent neighboring cells, instead of only four, better approximating a continuous landscape.

Road proximity was considered a potential confounding variable in this analysis. Roads and cleared linear features are associated with 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 resource selection function (RSF) to account

for the possibly confounding effect of vehicle avoidance on caribou habitat selection (Dyer and O'Neill 2002). To do this, we 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) to each cell.

Individual cells were also assigned a measure of digestible biomass (kg m^{-2} dry mass), weighted based on the composition of the caribou diet (Newmaster et al. 2013, Avgar et al. 2015), and wolf density (wolves/100 km^2) for each season (i.e., summer and winter) and year (2010–2013). Winter was defined as 1 November through 30 April (approximating the period of snow cover) and summer as 1 May through 31 October.

To estimate dietary digestible biomass, the biomass of terrestrial lichen, shrubs, forbs, grasses and mosses was measured in replicated 162 quadrats 625 cm^2 in area, sampled during the summer (Mallon 2014). Biomass values were converted to digestible biomass using acid detergent fiber (ADF) and neutral detergent fiber (NDF) measurements for each plant category using 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. 2015), 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. 2015). Land cover classes were based on the Ontario Provincial Far North Land Cover Database (FNLC v1.3.1; Ontario Ministry of Natural Resources 2013). These models were then projected across the landscape to generate estimates of dietary digestible biomass for every cell in the landscape (for further details see the supplementary mate-

rial in Avgar et al. [2015]).

Four wolf density kernels were calculated for winter (a different kernel for each winter between the winters of 2009–2010 and 2012–2013) using data from 32 packs, and three kernels were calculated for summer (2010–2012) using data from 34 packs (Kittle et al. 2015). Local wolf density (log transformed) was related to temporally-matched landscape characteristics for each season. The result was one model for summer wolf density and another for winter.

Landscape variables included seasonal NDVI, relative elevation, and land cover classes. Land cover classes were amalgamated into nine categories: water (open and turbid classes), open lowland (open fen, open bog, and freshwater marsh classes), treed lowland (treed peatland, treed fen, treed bog, and coniferous swamp classes), deciduous lowland (thicket swamp and deciduous swamp classes), deciduous upland (deciduous treed class), mixed upland (25–75% deciduous, 25–75% coniferous, and mixed treed class), sparse forest (sparse treed class), disturbed (disturbed treed/shrub and disturbed non/sparse classes; representing natural and anthropogenic disturbances), and newly disturbed (<1 year from fire or forestry disturbance). The coniferous treed class was withheld from the analysis and thus served as a reference class for the resulting inference. Cells were also characterized based on their proximity to dumps and settlement (if < 1 km, 1; otherwise, 0), their proximity to roads (if <500 km, 1; otherwise, 0), and their distance to shoreline of rivers or large lakes.

Generalized least squares regression models were fitted using the function gls in the R package nlme. Spatial autocorrelation was explicitly accounted for in the response variable. For each season, model fits were repeated 50 times on a different subset representing 2% of the total available data and taken at regular spatial intervals. Averaging the resulting 50 values for each coefficient allowed us to obtain robust coefficient estimates despite the inherent spatial autocorrelation in the data. Using encounter likelihoods as a proxy for risk has both advantages (measurability) and disadvantages (it does not account for ability of prey to modify their actual chances of mortality, given an encounter, through defensive investment). For more details, see Kittle et al. (2015) and Avgar et al. (2015).

One hundred and ten adult female caribou, located opportunistically within the study site, were fitted with GPS telemetry collars (7000 MA and 7000 SW collars from Lotek Engineering, Newmarket, Ontario, 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 10 days to 3 years (36 months), between March 2010 and March 2013. Potentially erroneous GPS fixes (i.e., leading to unreasonable speeds or round-trips) were removed. Further, the local-scale step selection analysis (SSF, described below; Fortin et al. 2005), required sequential GPS relocations in order to simulate available steps. GPS technology occasionally fails to record a fix at the specified interval. We 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 the caribou was not stationary (that is, time intervals over which a caribou's net displacement was exactly zero), were used. To appropriately compare local and seasonal scales of selection, seasonal scale selection analyses were also performed using this trimmed subset. The data were partitioned by individual, by year and by season. Two hundred and two individual-years for the summer season and 224 individual-years for the winter season were used.

To assess seasonal-range-scale selection for forage and avoidance of risk, we first assessed aggregate caribou space use behavior. We calculated an RSF following a used-available design (Manly et al. 2002), pooling data from all caribou to estimate selection patterns shared by the entire population. To calculate available points, we estimated seasonal ranges for each individual as the 95% minimum convex polygon (MCP) fitted to the full set of fixes throughout one season using the adehabitatHR package in R (Calenge 2006). We assumed GPS fixes to be used points and randomly drawn points within the seasonal ranges as available points. We included animal identity, per season, per year as a random effect on the intercept to account for unbalanced sample sizes and address spatial correlation (Breslow and Clayton 1993). No within-group correlation structure was used. We fit these mixed-effect RSF models as functions of the form

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

where $w(x)$ is relative probability of use, β_n is the estimated selection coefficient for covariate x_n, and γ_{0j} is the random per-subject intercept for individual j. As explanatory variables, we included dietary digestible biomass, wolf density and distance to roads. We estimated population-level RSFs for summer and winter separately to account for seasonal differences in resource distribution and resource needs.

To assess local scale selection patterns, we used a 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 generate available relocations, we calculated empirical distributions of turn angles and net distances traveled between GPS fixes (step lengths), pooling data from all caribou but splitting data between seasons. The distribution of 5-h step lengths, used to generate available fixes for the fine-scale selection analysis, was heavy-tailed. Most 5-h net displacements were <500 m but a few were much larger (up to 24.8 km in the summer and 35.3 km in the winter; Fig. 2A). Caribou had a roughly uniform distribution of turn angles (Fig. 2B).

For every GPS fix in the analysis, we generated 10 available relocation points using randomly drawn turn angles and distances from the empirical distribution for the appropriate season. As before, we assessed fine scale habitat selection for each season by estimating one conditional logistic regression (for details see Fortin et al. 2005) per season for all caribou, using caribou ID as a random effect. We used the same three variables as in the coarse-scale analysis, with one modification. 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.

Finally, we calculated one SSF and one RSF as described above for each caribou in each season in each year. These models represented selection for biomass and avoidance of risk for each individual caribou relative to what was available to only that animal. To compare the consistency
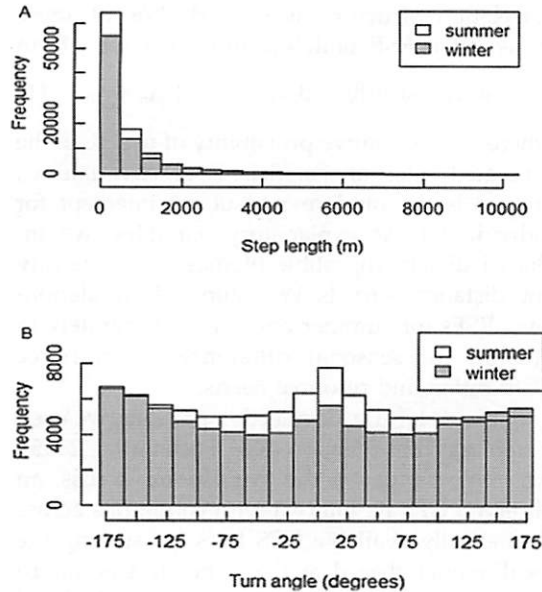
Fig. 2. Summer (white) and winter (grey) distributions of step lengths (A) and turn angles (B) over 5 h intervals. The median step length was 299.3 m in summer and 301.1 m in winter. Step length bins with 50 or fewer steps were not shown.

of selection behavior across scales, we then used linear regression to compare the coefficients of selection for forage and avoidance of risk by each individual at the local scale to that at the seasonal scale.

RESULTS

Caribou experienced a wide range of conditions on this landscape. In the summer ranges, average digestible biomass values varied from 0.014 to 0.037 kg m^{-2} dry weight and average wolf density values varied from 0.205 to 0.286 wolves/100 km^2. In the winter, digestible biomass values ranged from 0.022 to 0.063 kg m^{-2} dry weight and relative wolf density values ranged from 0.200 to 0.295 wolves/100 km^2. At seasonal-range scales (Fig. 3) and at local scales of selection (Fig. 4), caribou selected for habitats that are high in dietary digestible biomass, avoided habitats that typically have high wolf density, and avoided areas near roads in both the summer and the winter. Note that that the magnitude of resource selection coefficients was

much smaller at the fine scale than at the coarse scale. On the other hand, local scale selection coefficients were significantly related to coarse scale coefficients in both seasons for both forage and risk (Fig. 5).

DISCUSSION

Caribou selected for high biomass and avoided predation risk at both local and seasonal scales of selection, indicating that, regardless of scale, forage and risk play important roles in shaping caribou space use. Moreover, selection for forage and avoidance of risk at seasonal was predicted by an individual's local scale selection for forage and avoidance of risk. This suggests that caribou responded to availability in qualitatively similar ways at both scales. These results clearly support the scaling-up hypothesis and reject the scale-dependent fitness hypothesis.

Ecologists aim to both understand fine-scale behaviors using relatively coarse data and to predict coarse-scale patterns (i.e., population persistence) using relatively fine-scale data (Gaillard et al. 2010, Morales et al. 2010, Owen-Smith et al. 2010). Because selection patterns can change across scales (DeCesare et al. 2012), it is imperative to understand the relationship between patterns observed at multiple spatio-temporal scales.

Differences in selection patterns between spatio-temporal scales have been noted in species ranging from barren-ground grizzly bears (*Ursus arctos*; Ciarniello et al. 2007) to birds (Orians and Wittenberger 1991). Elk have different preferences for key landcover classes at different spatio-temporal scales (Boyce et al. 2003). Moose and caribou have been observed to select for safety from predation at coarse scales and forage at finer scales (Rettie and Messier 2000, Dussault et al. 2005). On the other hand, some authors have demonstrated fundamental similarities between selection at different scales. Musk oxen, for example, select for the same forage items across multiple spatio-temporal scales (Schafer and Messier 1995). However, this appears to be the exception to the rule.

There have been many advances in interpreting and predicting differences in selection across spatio-temporal scales, starting with Johnson's (1980) assertion that selection operates differently
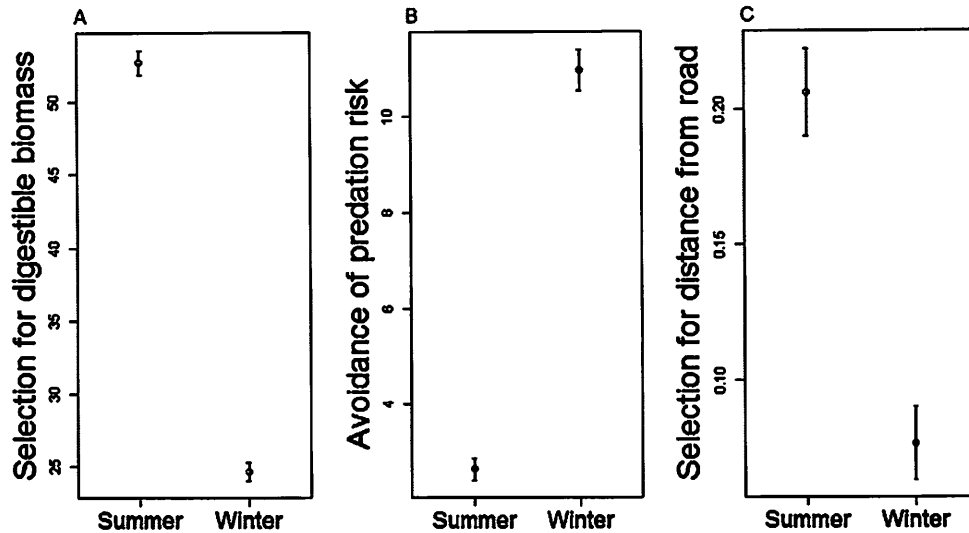
Fig. 3. Coarse scale selection coefficients for digestible biomass (A), avoidance of predation risk (B), and selection for distance away from the nearest road (C). The bars represent the 95% confidence intervals around the selection coefficients.

at four different hierarchical scales. Rettie and Messier (2000) claimed that the differences between habitat selection at different scales is predictable—animals will select the factors that most limit fitness at the coarsest spatio-temporal scales and will select for other factors at finer scales. This prediction was borne out in studies on moose (Dussault et al. 2005) and migratory elk (Hebblewhite and Merrill 2009). A number of authors (Johnson et al. 2002, Fryxell et al. 2008)
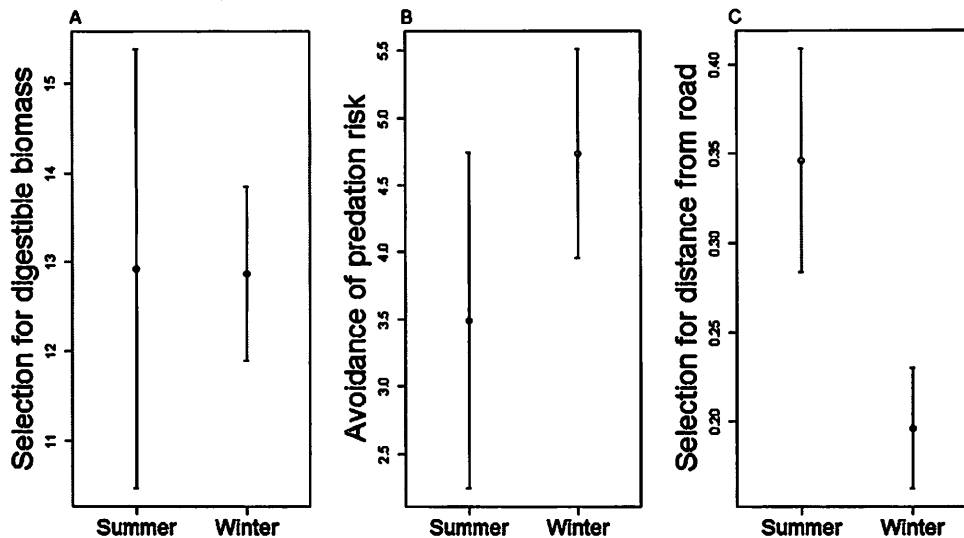

Fig. 4. Fine scale selection coefficients for digestible biomass (A), avoidance of predation risk (B), and selection for distance away from the nearest road (C). The bars represent the 95% confidence intervals around the selection coefficients.

Selection for biomass
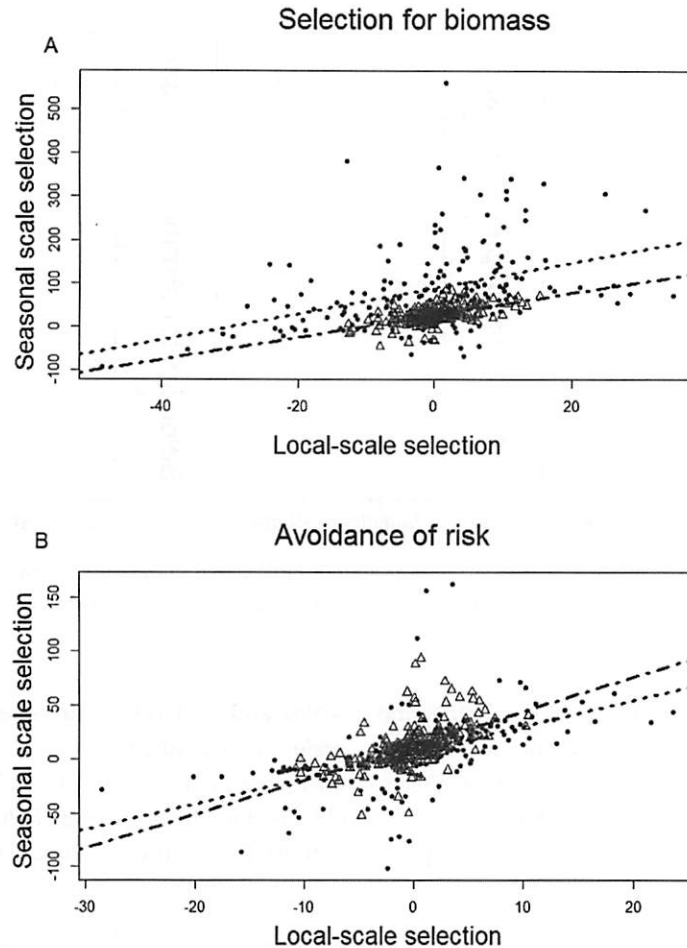
A

Avoidance of risk

B

Fig. 5. The relationship between seasonal scale and local scale selection for forage (A) and avoidance of risk (B) in the summer (circles) and the winter (triangles). Lines indicate significant regression slopes for the summer (β = 2.986, $P < 0.001$, $r^2 = 0.145$ for biomass selection and $\beta = 2.564$, $P < 0.001$, $r^2 = 0.321$ for risk avoidance) and winter ($\beta = 2.388$, $P < 0.001$, $r^2 = 0.280$ for biomass selection and $\beta = 3.159$, $P < 0.001$, $r^2 = 0.317$ for risk avoidance).

have demonstrated that differences in selection patterns between scales may arise from different movement modes (and different objectives, such as foraging or traveling) at different scales. Other authors aim to find a characteristic scale at which selection is most pronounced (Holland et al. 2010, de Knegt et al. 2011). Regardless of scale, however, animals select habitats high in forage biomass and low in risk, when possible (Rettie and Messier 2000, Owen-Smith et al. 2010). By focusing on these key variables, we found a correlation between selection patterns of caribou at different spatio-temporal scales.

There are many possible interpretations of the positive correlation between scale-specific patterns of resource selection observed here for woodland caribou. One interpretation is that habitat selection results from foraging decisions, provided that both scales of selection reflect the same behavioral mode and decision-making framework (i.e., foraging rather than searching; Getz and Saltz 2008) or the same ecological domain (Wiens 1989). According to this view, space-use decisions made by individuals should scale up to generate similar selection patterns at coarse scales, such as the patterns of resource

selection observed in this study (Owen-Smith et al. 2010). An alternative interpretation is that patterns of resource selection at different spatio-temporal scales may operate independently of one- another (Orians and Wittenberger 1991, Rettie and Messier 2000). According to this interpretation, the observed similarity between local and seasonal selection by woodland caribou is a result of independent selection at both scales driven by similar resource requirements (Hins et al. 2009). Finally, 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).

Though caribou exhibited similar patterns of selection at both scales, the SSF selection coefficients were generally much smaller than the RSF coefficients. The landscape studied here has wide global gradients of availability (Fig. 1)—larger spatial scales encompass more landscape variability than smaller spatial scales. Thus, selection for all features important to survival may be carried out simultaneously at larger spatial scales to capitalize upon this variability, and caribou selection strengths at fine scales may be limited by lack of variability. Further studies must be carried out to better understand why caribou appeared less selective at fine spatio-temporal scales.

Complex predictive models of resource distribution, extrapolated over a large spatial domain, are often models that perform poorly (Barry and Elith 2006). Considerable effort has gone into ensuring that our models are satisfactory (for more information, see Kittle et al. [2015] and Avgar et al. [2015]). Importantly, the use of biomass and wolf density as variables for this study allowed us to directly assess and interpret caribou's responses to forage and risk across a broad landscape. Most previous studies of resource selection in the published literature use land cover classes and abiotic or satellite-gathered data as predictor variables, followed by speculation about the resources represented by specific land cover classes. Our approach differs from much of the current literature by calibrating landscape features with respect to relative resource abundance and safety, reducing the amount of post-hoc speculation needed to interpret the results.

Provided caution is exercised, we submit that use of variables representing actual needs or risks represent a step forward in interpreting resource selection functions that offers stronger inference about putative causal factors. Nonetheless, we recognize that forage biomass and probability of wolf presence are just one component of an animal's forage and safety needs, respectively. Animals may be driven to select either carbon-rich or nitrogen-rich foods, for example, and they may seek to avoid detection or seek to improve their chance of escape, rather than avoiding predator presence altogether (DeCesare et al. 2014).

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. Predicting these changes in habitat selection is key to understanding observed shifts in habitat needs between pristine and disturbed landscapes (Osko et al. 2004). The relationship between selection at multiple spatial scales is still poorly understood (Mayor et al. 2009). To further our understanding, further comparisons between very fine local selection and coarse, seasonal selection must be undertaken, with particular attention to using variables closely related to an animal needs. Understanding how animal populations respond to the landscape across multiple spatial scales will enable us to better predict land use and movement.

ACKNOWLEDGMENTS

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