Landscape-level wolf space use is correlated with prey abundance, ease of mobility, and the distribution of prey habitat

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Abstract. Predator space use influences ecosystem dynamics, and a fundamental goal assumed for a foraging predator is to maximize encounter rate with prey. This can be achieved by disproportionately utilizing areas of high prey density or, where prey are mobile and therefore spatially unpredictable, utilizing patches of their prey’s preferred resources. A third, potentially complementary strategy is to increase mobility by using linear features like roads and/or frozen waterways. Here, we used novel population-level predator utilization distributions (termed “localized density distributions”) in a single-predator (wolf), two-prey (moose and caribou) system to evaluate these space-use hypotheses. The study was conducted in contrasting sections of a large boreal forest area in northern Ontario, Canada, with a spatial gradient of human disturbances and predator and prey densities. Our results indicated that wolves consistently used forest stands preferred by moose, their main prey species in this part of Ontario. Direct use of prey-rich areas was also significant but restricted to where there was a high local density of moose, whereas use of linear features was pronounced where local moose density was lower. These behaviors suggest that wolf foraging decisions, while consistently influenced by spatially anchored patches of prey forage resources, were also determined by local ecological conditions, specifically prey density. Wolves appeared to utilize prey-rich areas when regional preferred prey density exceeded a threshold that made this profitable, whereas they disproportionately used linear features that promoted mobility when low prey density made directly tracking prey distribution unprofitable.

Key words: Alces alces; Canis lupus; functional response; predator–prey game; Rangifer tarandus caribou.

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INTRODUCTION

Predators influence survival, demography, and the spatial distribution of their prey through direct predation and the non-lethal risk of predation (Ripple et al. 2014), processes influenced by predator space-use patterns (Kauffman et al. 2007, McPhee et al. 2012a, Middleton et al. 2013). The rate at which a predator encounters prey is central to predator movement patterns (Lima and Dill 1990), underlies the functional response, and is key to understanding predator-prey dynamics (Holling 1959). The most intuitive way to maximize encounter rate is to exploit areas of high prey density (Carbone and Gittleman 2002). However, mobile prey can be spatially unpredictable, so an alternate strategy is to track areas where prey foraging habitat is abundant (Mitchell and Lima 2002). Terminant "leap-frogging" (Sih 2005), prey habitat hypothesis, although predicted by tri-trophic foraging models that allow predators and prey to move and respond to each other’s movements (Iwasa 1982), has rarely been empirically tested (Hammond et al. 2007), particularly at large spatial scales (Flaxman and Lou 2009). A third strategy is for predators to improve mobility across the landscape (Avgar et al. 2011), which can have a significant positive impact on kill rate (McPhee et al. 2012a, Vander Vennen et al. 2016). An enhanced understanding of the processes driving landscape-level predator spatial behavior allows for the advancement of ecological theory (Lima 2002) and is necessary to effectively manage populations increasingly impacted by anthropogenic activities.

Here, we used a novel population-level approach ["localized density distributions (LDDs)"] generated from Global Positioning System (GPS) telemetry data from 30 wolf (Canis lupus) packs to empirically investigate second-order (Johnson 1980) predator space-use behavior in a system with wolves, moose (Alces alces), and woodland caribou (Rangifer tarandus caribou) in northern Ontario, Canada. We compared two study sites exhibiting contrasting levels of anthropogenic impact (disturbed vs. undisturbed) as well as differing prey and predator densities. Our objective was to investigate which alternate hypothesis—prey distribution, the distribution of prey preferred habitat, or predator mobility—most influenced observed broad-scale patterns of wolf space use within these contrasting areas.

If predators directly track prey, then wolves should disproportionately utilize landscape regions with high moose and caribou abundance. If predators track prey habitat, wolf space use should be centered in locations with prey preferred habitat regardless of actual prey density. Recent research in our study area showed that moose prefer forest stands dominated by mixed or deciduous species and post-harvest stands dominated by early-successional plant species (Street et al. 2015), echoing similar findings elsewhere in eastern Canadian boreal forests (Dussault et al. 2005, Brown 2011). Recent radiotelemetry research on woodland caribou in boreal forests of Ontario overwhelmingly indicates that caribou prefer stands dominated by mature conifer and sparse forest (Avgar et al. 2013, 2015, Hornseth and Rempel 2016). Finally, if predator mobility underlies wolf space use, then wolves should exploit linear features that increase landscape permeability and encounter rates with prey, such as roads and frozen waterbodies (Musiani et al. 1998, Latham et al. 2011).

MATERIALS AND METHODS

Study area

The research was conducted at two sites separated by <100 km within a 40,000-km² study area in northern Ontario’s Shield Eco-zone (Crins et al. 2009; Fig. 1). The southeast site (86°32’ W, 50°57’ N to 88°33’ W, 49°49’ N), centered on Nakina township, is characterized by substantial anthropogenic disturbance, whereas the northwest site (89°51’ W, 52°6’ N to 92°1’ W, 51°1’ N), centered on Pickle Lake township, is relatively pristine (Fig. 1; see Kittle et al. 2015 for full study site description). The difference is predominantly due to active timber
harvest operations around Nakina but not Pickle Lake, which is beyond the current northern limit of licensed timber extraction (51° N). At the disturbed Nakina site, the density of primary and secondary roads is 0.075 km/km² and of tertiary roads (e.g., forestry roads) 0.449 km/km², compared to 0.012 and 0.018 km/km², respectively, at the undisturbed Pickle Lake site. Anthropogenically disturbed forest areas are smaller and more uniformly distributed at Nakina, but comprise a larger portion of the landscape than at Pickle Lake (23.5% vs. 9%), where the majority of total disturbance was from three major wildfires >20,000 ha each (Fig. 1). Timber extraction has affected forest composition at the landscape scale, with undisturbed coniferous forest comprising only 18.5% of the land cover at Nakina and 38.2% at Pickle Lake. Wolf density estimates were 5.1 wolves/1000 km² at the disturbed Nakina site and 3.1 wolves/1000 km² at the undisturbed Pickle Lake site (Kittle et al. 2015). Moose are the most abundant ungulate at both sites, with aerial surveys indicating average density at the disturbed site twice that at the undisturbed site (Kittle et al. 2015). Caribou are usually secondary prey for wolves where sympatric with moose (Seip 1992), as they are here and throughout much of the boreal forest. Nonetheless, wolves are the main predator of woodland caribou throughout most of North America (McLoughlin et al. 2003).

**Telemetry data collection**

Between January 2010 and January 2013, 49 wolves were tracked using GPS telemetry collars (Lotek 7000MA, 7000SAW, Lotek Wireless, Newmarket, Ontario): 34 individuals representing 19 packs and three lone individuals (satellites) at the disturbed site and 15 wolves representing 11 packs and two satellites at the undisturbed site (Appendix S1: Table S1; see Kittle et al. 2015 for
complete collaring details). Wolf relocations were recorded every 2.5–5 h, with fix rate success 91% (range: 77–99%, n = 17; Anderson 2012), meaning resource utilization analyses were likely unbiased (Frair et al. 2004). During this period, 124 woodland caribou, 60 at Nakina and 64 at Pickle Lake, were fitted with GPS telemetry collars (Lotek 7000MA, Iridiumtrack 3D, Lotek Wireless, Newmarket, Ontario, Canada). Caribou relocations were recorded every 2.5, 5, or 25 h. Animal handling and care was approved by University of Guelph's Animal Utilization Protocol and the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (protocols 10/11/12-183 for caribou and 10/11/12-218 for wolves).

Landscape-level utilization distribution

We developed pooled winter (1 November to 30 April) population-level utilization distributions (UDs) for wolves for each study site. Wolf telemetry relocations were sub-sampled at five-hour fix intervals across individuals to eliminate possible bias resulting from unequal relocation intervals. When packs had >1 collared individual in a single winter, we used the relocations from the individual whose collar was operational for the maximum portion of the winter (primary individual), only supplementing with data from another animal for those periods when the primary individual’s collar was not operational (either yet to be put on or no longer transmitting) in order to maximize coverage duration for each pack (Appendix S1: Table S1). We used fixed-kernel density estimates (kde), to develop UD (100 × 100 m cell size) for each pack during each year (adehabitatHR in R). The smoothing bandwidth was determined by reducing the reference bandwidth sequentially by 0.1 to the point just prior to where the 99% volume UD (vUD) fragments into multiple polygons (Mills et al. 2006, Berger and Gese 2007, Jacques et al. 2009, Kie 2013).

We converted kernel UD (kUDs) to vUDs, subtracted vUD values from 100 for a more intuitive measure for each cell and integrated to 1 for each pack to remove bias imposed by differing home range sizes (Kittle et al. 2015). We then multiplied by pack size as estimated during collaring and/or follow-up monitoring. When individual packs were sighted multiple times during a winter, pack size estimates were averaged to determine a single pack size for that winter, thus incorporating the possibility of intra-seasonal individual pack size variation. If multiple packs’ ranges overlapped single cells on the landscape, values were summed to determine the cumulative cell value for each year. We then integrated to 1 for each winter/year by dividing each cell’s cumulative value by the sum of all pack-weighted cell values in the UD. The resulting values represented winter wolf probability densities in each spatial cell, but because they were weighted by group size, they were not true probability density functions and could not be termed UD in the formal sense (Jennrich and Turner 1969). Instead, we considered these layers as LDDs.

The above process was repeated for each year for both study areas. We then amalgamated individual-year LDDs by combining values across years and dividing by the number of years that a given cell was used. This final combined year LDD was standardized to ensure a maximum cell value of 1 by dividing each cell value by the maximum value of all cells (Zuur et al. 2007). We removed cells with values <0.05 to minimize any potential bias arising from the presence of un-collared packs in the study sites. This resulted in 95% population-level LDDs comprising 21,066 relocations from 19 packs and three satellites covering 18,349 km² at Nakina, and 9034 relocations from 11 packs and two satellites covering 19,439 km² at Pickle Lake (Appendix S1: Table S1; Fig. 2).

Model variables

We conducted fixed wing aerial surveys (15 February–13 March 2011, at Pickle Lake and 25 January–03 March 2012, at Nakina) to estimate moose abundance throughout both study sites (Street et al. 2015). Survey flight lines were oriented north–south, 5 km apart covering >21,000 km² at each location. When moose or their fresh tracks were detected, observers deviated from the flight path to record accurate locations. The flight path was then rejoined from where it had been left. Only observed moose were included in density estimates.

To match wolf-use data with the coarse-resolution moose data, we overlaid the aerial survey extent with a grid of 5 × 5 km² cells, with grid pixels centered on the aerial survey lines. We then determined the mean wolf LDD value for each 25-km² cell completely covered by the 95% population-level wolf LDD.
To estimate relative moose availability across the landscape, we counted all moose detected along the 5-km transect length bisecting each cell and assigned this value, effectively proportional to moose density, to each cell. We estimated caribou use by summing the winter relocations of GPS-collared caribou (Avgar et al. 2015) in each 25-km² cell for each study site. Using a fixed relocation interval of 25 h to ensure inclusion of the maximum number of collared caribou and eliminate sampling bias, we used 13,653 relocations from 60 individuals at Nakina and 21,439 relocations from 64 individuals at Pickle Lake. We assumed that the relative use of different habitats by caribou collared randomly across each site reflected actual differences in caribou abundance among habitat types.

We determined land-cover composition using the 30 × 30 m resolution (Ontario Provincial Far North Land Cover Database, FNLC v1.3.1, Ontario Ministry of Natural Resources 2013). This map did not extend south of the Pickle Lake study site, so we merged it with the most recent Ontario Land Cover map (Spectranalysis Inc. 2004) where necessary. Maps included updated disturbances (both fire and harvest) through 2009. We amalgamated land-cover types into four relevant classes reflecting preferred forage resources for moose (deciduous/mixed upland and disturbed) and caribou (sparse treed and coniferous treed, Table 1). Preferred forage resources for moose were determined by global (Peek et al. 1976, Belovsky 1981, Dussault et al. 2005) and regional research (Brown 2011, Street et al. 2016) as well as an independent resource selection analysis of moose within the study area (Street et al. 2015). In this latter study, deciduous forest was the reference class with all other classes showing negative selection coefficients relative to this class, which indicates clear preference for deciduous forest (Street et al. 2015). Both mixed and disturbed forest classes had coefficient values close to 0 and were sufficiently similar to deciduous forest in terms of selection coefficients to be eliminated.

Fig. 2. Landscape-level 95% winter localized density distributions for wolf packs in the undisturbed northwest (Pickle Lake) and disturbed southeast (Nakina) sites within the study area. Eleven wolf packs and two satellite individuals encompassing 9034 telemetry relocations were used to determine the northwest utilization distributions (UD) and 19 wolf packs and three satellite individuals encompassing 21,066 telemetry relocations for the southeast UD. Blue represents water bodies with Lake Nipigon prominent in the southwest corner.
from the final model (Street et al. 2015). We then determined the proportion of each land-cover class enclosed by each grid cell. We amalgamated primary roads, secondary roads, and railways into a single category (primary) as these included the majority of maintained corridors. The remainder, tertiary roads, were combined with utility lines. Road densities (m/cell) were then determined for each category. We converted rivers and lake-shores, derived from digital image maps (Major Water Regions Ontario, DMTI Spatial, Markham, Ontario, Canada), into vector data and measured the density of these linear water features as m/cell. The proportion of open water/cell was determined in the same manner as the land-cover variables.

There was a scale discrepancy between prey habitat, measured at a 30-m$^2$ resolution, and moose abundance, measured at a 25-km$^2$ resolution. This asymmetry is typical of resource selection/utilization studies (Boyce 2006) and is often unavoidable due to logistical constraints, but can potentially influence results. The finer resolution of the habitat data allows increased precision in comparison with the coarse-grained moose data as well as greater variability, which might allow for the detection of more nuanced selection patterns. We minimized this disparity by amalgamating land-cover classes into broad categories that were then determined as proportional variables of the coarser (25-km$^2$) cell.

**Statistical modeling**

We used generalized least-squares mixed-effects regression models (gls in R package nlme) to link LDDs to predictor variables allowing us to account for spatial autocorrelation in the response variable (Zuur et al. 2009). Plotting semi-variograms for un-structured gls models indicated the expected spatial correlation and provided a starting point (range and nugget) from which to inform spatially structured models (Crawley 2007). We tested various correlation structures using a restricted maximum-likelihood (REML) approach on a model fully loaded with all candidate predictor variables, and we used Akaike’s information criterion (AIC) to determine the most parsimonious model to apply to our data (Zuur et al. 2009). We used semi-variograms of normalized residuals, plots of normalized residuals against fitted values, and Q–Q plots to verify that rational quadratic spatial correlation (corRatio in nlme) dealt most effectively with the spatial autocorrelation in our response (Crawley 2007). To address heteroscedasticity, we conducted a Box–Cox power transformation ($\lambda = \frac{1}{4}$) of the response variable (Zuur et al. 2007). We square-root-transformed the moose count data, caribou relocation variable, and road variables (after adding 0.5 to each value to account for 0s in the data) to comply with statistical assumptions. We log-transformed the open water proportion variable to address heteroscedasticity (Zuur et al. 2007) and conducted correlation analysis to ensure that independent variables were not highly correlated ($r < 0.7$; Dormann et al. 2013).

We then conducted a two-step modeling procedure, first determining the best model with which to represent each of our three proposed hypotheses (prey abundance, prey habitat, and predator mobility). We used backward stepwise variable elimination using likelihood ratio tests to reduce
each hypothesis-specific global model (Table 1) to the best model for each hypothesis (Zuur et al. 2009). Akaike’s information criterion can only be used to compare REML models with identical fixed variables, so we used gls with maximum likelihood to determine the best model for each and then re-ran it in REML to ensure unbiased final model coefficient estimates (Zuur et al. 2009). To test our hypotheses, we compared the best models for each hypothesis, as determined from the backward stepwise procedure (PREY = prey abundance; HABITAT = prey habitat/resources; MOBILITY = predator mobility), as well as all their additive combinations and a null model. This final model suite therefore consisted of eight models for each study area. We used ΔAIC to rank models and Akaike weights (wi) to determine the likelihood of each model given the assumption that one of the models in the set was the best (Burnham and Anderson 2002). We estimated the relative importance of predictor variables by summing wi across all models in the set where each variable occurred, ensuring equal variable representation for valid comparisons (Burnham and Anderson 2002). We used model averaging with unconditional standard errors for final coefficient estimation as this increases precision and reduces bias compared to single model estimates (Burnham and Anderson 2002). The inferred strengths of associations were therefore based on these model-averaged coefficient estimates and associated standard errors such that strongly selected variables did not have confidence intervals overlapping zero.

Finally, we conducted sensitivity analysis of the best models in each study area by plotting the projected localized wolf density distribution value against each individual input variable comprising each top model and estimating Pearson’s correlation coefficients. This provided a visual and additional statistical means to indicate the relative influence of individual explanatory variables. Statistical and spatial analysis was undertaken using R software version 2.15.1, R Development Core Team 2012, ArcMap 10.3.1 (ESRI 2015) and Geospatial Modeling Environment 0.7.2.0 (Beyer 2012).

RESULTS

Deciduous/mixed forest was represented in both top HABITAT models and was strongly positively associated with probability of wolf use (Table 2), suggesting that wolves actively select for this important moose foraging habitat. Disturbed forest, another habitat type preferentially selected by moose, was also strongly positively associated at the disturbed site, whereas sparse forest was retained in the top model for the undisturbed site, expressing a weak negative association. Coniferous forest, which comprises the majority of the boreal forest landscape, exerted minimal influence on wolf landscape utilization at both study sites and was dropped during stepwise model competition.

Moose abundance was included in the top PREY model for the disturbed study site and was strongly positively associated with the probability of wolf use (Table 2), suggesting that in this relatively moose-rich landscape wolves are directly tracking these key prey. At the undisturbed site where moose abundance is lower, this variable

<table>
<thead>
<tr>
<th>Study area</th>
<th>Model</th>
<th>Variable</th>
<th>0</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nakina</td>
<td>PREY</td>
<td>Moose density††</td>
<td>0.019934</td>
<td>0.007060</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Caribou relocations†</td>
<td>−0.002375</td>
<td>0.001258</td>
</tr>
<tr>
<td></td>
<td>HABITAT</td>
<td>Deciduous/mixed forest††</td>
<td>0.085006</td>
<td>0.031716</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Disturbed††</td>
<td>0.064897</td>
<td>0.019880</td>
</tr>
<tr>
<td></td>
<td>MOBILITY</td>
<td>Primary road density</td>
<td>0.000047</td>
<td>0.000089</td>
</tr>
<tr>
<td>Pickle Lake</td>
<td>PREY</td>
<td>Caribou relocations</td>
<td>−0.001549</td>
<td>0.001414</td>
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<tr>
<td></td>
<td>HABITAT</td>
<td>Deciduous/mixed forest††</td>
<td>0.163640</td>
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</tr>
<tr>
<td></td>
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<td>Sparse forest</td>
<td>−0.192980</td>
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<tr>
<td></td>
<td>MOBILITY</td>
<td>Open water proportion††</td>
<td>0.016353</td>
<td>0.004709</td>
</tr>
</tbody>
</table>

Note: The response variable was the localized density distribution value transformed using a Box-Cox power transformation (k = 1/4).
††† Unbiased 90%/95% confidence intervals do not overlap 0.
was not influential and the top prey model here included only the caribou use parameter. Caribou use was included in the top PREY model for the disturbed site, but with a strong negative association, indicating spatial separation between wolves and caribou here.

For the disturbed site, only primary road density was retained in the top MOBILITY model, although selection for this variable was not convincing (Table 2). At the undisturbed site, where road density was much lower, these anthropogenic features were not included in the top MOBILITY model. Instead, wolves appeared to disproportionately utilize areas of open water (i.e., frozen lakes).

The best overall model differed across study sites. The PREY + HABITAT model was ranked the best for the disturbed site (McFadden's $R^2 = 0.32$), whereas the HABITAT + MOBILITY model was ranked the best for the undisturbed site (McFadden's $R^2 = 0.25$; Table 3). In both locations, however, the global model (PREY + HABITAT + MOBILITY) had $\Delta$AIC values <2, indicating that this more inclusive model was also competitive. Sensitivity analysis indicated that the negative association of wolves with caribou telemetry relocations was the most influential variable in the top model for Nakina (Fig. 3), whereas the proportion of deciduous and mixed forest was most influential for Pickle Lake (Fig. 4). When comparing hypotheses directly, HABITAT had strong influence on wolf use for both study sites, PREY was equally influential to HABITAT for the disturbed site, and MOBILITY was highly influential for the undisturbed site (Fig. 5). For the disturbed site, summed $w_j$ scores for models including HABITAT and/or PREY were >3× those for models including MOBILITY, whereas for the undisturbed site, HABITAT and/or MOBILITY models had summed $w_j$ scores >2× those for models including PREY (Fig. 5).

Together, this suggests that in the relatively prey-rich disturbed site, wolves were tracking their preferred prey and that prey’s preferred habitat, but not basing movement decisions on the need to increase mobility across the landscape. In contrast, in the relatively prey-poor undisturbed site, rapid movement across the landscape, using available natural features, appears an important factor underlying wolves’ space-use decisions, as does the location of spatially anchored moose habitat. Wolves here did not appear to track prey directly. Coefficient estimates were stable across models, particularly for those variables represented in the best models for each study area (Table 4).

**DISCUSSION**

Our results further support recent evidence that wolves adapt their spatial behavior to suit local ecological conditions (Courbin et al. 2013, Kittle et al. 2015). At the disturbed site, where relative moose density was higher, wolves disproportionately used areas of high moose abundance, possibly as a way to maximize their encounter rate with prey. At the undisturbed site, where moose density was lower, wolves used increased mobility as a strategy to potentially increase prey encounter rate, given that their preferred prey (i.e., moose) were fewer and therefore more difficult to access directly. This could suggest foraging behavior that is mediated by a threshold in prey density. Under this scenario, wolves can target

**Table 3. Model comparison table with $\Delta$AIC, Akaike weights ($w_j$), and relative rank.**

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$AIC</th>
<th>$w_j$</th>
<th>Nakina Rank</th>
<th>$\Delta$AIC</th>
<th>$w_j$</th>
<th>Pickle Lake Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREY</td>
<td>10.339</td>
<td>0.004</td>
<td>5</td>
<td>19.119</td>
<td>0.000</td>
<td>7</td>
</tr>
<tr>
<td>HABITAT</td>
<td>6.839</td>
<td>0.022</td>
<td>3</td>
<td>10.533</td>
<td>0.003</td>
<td>6</td>
</tr>
<tr>
<td>MOBILITY</td>
<td>21.856</td>
<td>0.000</td>
<td>7</td>
<td>6.366</td>
<td>0.024</td>
<td>3</td>
</tr>
<tr>
<td>PREY + HABITAT</td>
<td>0.000</td>
<td>0.676</td>
<td>1</td>
<td>9.379</td>
<td>0.005</td>
<td>5</td>
</tr>
<tr>
<td>HABITAT + MOBILITY</td>
<td>8.250</td>
<td>0.011</td>
<td>4</td>
<td>0.000</td>
<td>0.569</td>
<td>1</td>
</tr>
<tr>
<td>PREY + MOBILITY</td>
<td>10.696</td>
<td>0.003</td>
<td>6</td>
<td>6.402</td>
<td>0.023</td>
<td>4</td>
</tr>
<tr>
<td>PREY + HABITAT + MOBILITY</td>
<td>1.734</td>
<td>0.284</td>
<td>2</td>
<td>0.829</td>
<td>0.376</td>
<td>2</td>
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<tr>
<td>NULL</td>
<td>24.308</td>
<td>0.000</td>
<td>8</td>
<td>21.430</td>
<td>0.000</td>
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</tbody>
</table>

*Notes: AIC, Akaike’s information criterion. Top models for each study site are highlighted.*
preferred prey directly when prey are abundant but, where prey are scarce, wolves focus more on features that allow for rapid movement across the landscape to improve encounter rate. Areas of abundant moose forage, in the form of deciduous and mixed forest, were heavily utilized across sites. Forest stands recently disturbed by harvesting provide abundant forage for moose in the form of early-successional deciduous plants (He et al. 2002). Such stands were widely available at the Nakina study area and heavily utilized by wolves as a consequence. The selection by wolves of habitat preferred by their prey may be a beneficial strategy irrespective of prey density, because it is a spatially predictable way to maximize prey encounters compared to searching for prey directly and less energetically costly than rapid movement across large areas of an often snow-covered landscape.

The observed selection by wolves for deciduous and disturbed forest stands typically used by moose supports the prey habitat hypothesis. These observations are consistent with Sih's (2005) “leap-frogging” hypothesis, loosely based on a shell game between predators and prey in which each moves according to fitness-maximizing

Fig. 3. Sensitivity analysis of input variables comprising the best wolf space-use model at Nakina. The far left graph shows localized density distribution values projected from the top Nakina model (PREY + HABITAT) against the square root of moose density input variable values (Pearson’s correlation $|r| = 0.43$). The inside left graph shows the same model output on the $y$-axis against the square root of caribou relocations input variable values ($|r| = -0.73$). The inside right graph shows the same model output on the $y$-axis against the proportion of deciduous/mixed forest input variable values ($|r| = 0.37$), whereas the far right graph shows the same model output against the proportion of disturbed forest input variable value ($|r| = 0.54$). Both the visual pattern and the Pearson’s correlation coefficients indicate that the location of caribou telemetry relocations is the more influential variable. All correlations are significant ($P < 0.0001$).
To our knowledge, our study presents the first direct empirical support of this prediction at such a broad scale. Previous arguments in support of the leap-frogging hypothesis have come from individual-based predator movement studies (Huggard 1993, Kunkel and Pletscher 2001, Gurarie et al. 2011). For example, Alberta wolves selected reliable elk \((Cervus elaphus)\) locations when white-tailed deer \((Odocoileus virginianus)\) were widely spaced across the landscape, despite there being comparatively fewer elk groups available (Huggard 1993). However, whether this shows that wolves were selecting elk habitat or elk themselves could not be assessed. Kunkel and Pletscher (2001) found that wolves selected areas favored by deer and preferentially hunted in deer wintering areas but whether this was due to higher deer abundance in these locations or the predictability of the prey's resources was unclear. Similarly, lions \((Panthera leo)\) in South Africa concentrated kills around waterholes, turning this critical prey habitat, typically associated with high prey abundance, into passive traps (Davidson et al. 2013). At a finer scale, Courbin et al. (2014) found that wolf distribution aligned more closely with highly connected network nodes of their prey than with prey spatial distribution. Herein, network nodes represented the most strongly selected habitat patches of moose and caribou.

That moose abundance does not precisely mirror areas of preferred moose forage is not surprising. Foraging models allowing for predator and prey movement often predict that the best prey strategy is to bias movement toward higher-quality food patches without completely
committing to them (Mitchell and Lima 2002). This makes prey individuals spatially unpredictable, consistent with the leap-frogging strategy. In turn, prey distribution is theoretically more likely to approach uniformity since predator presence in a preferred foraging patch equalizes that patch’s benefit with one of lower quality but lower risk (Bednekoff 2007). Although not explicitly tested here, the low correlation between relative moose density and preferred moose forage resources ($r = 0.08$ for deciduous upland and $r = 0.19$ for disturbed forest at the disturbed site and $r = -0.01$ and $0.20$, respectively, at the undisturbed site) suggests that moose were indeed spatially unpredictable at this broad scale.

An alternative explanation for why wolves at the undisturbed site did not selectively use areas of high moose abundance was because the lower overall moose density at the Pickle Lake study site constrained wolves, as generalist predators, from treating moose as preferred prey. Wolf diet selection has been shown to vary with large herbivore abundance in Italy (Meriggi et al. 1996) and Poland (Jedrzejewski et al. 2000). However, wolves at Pickle Lake strongly selected for moose foraging habitat and all wolf kills located from GPS cluster analysis at this site were moose ($N = 21$; Vander Vennen et al. 2016), indicating a prey preference. Therefore, it remains most likely that the low moose density at the Pickle Lake site rendered wolves’ attempts to exploit areas of high moose abundance futile, forcing them to rely on the predictable areas of moose forage together with increased mobility across frozen lakes. That wolves at Pickle Lake did not select for disturbed forest, which represents high-quality moose forage, may have resulted from its limited and clumped distribution (Fig. 1) restricting this habitat’s availability to territorial wolves.

Wolves have been shown to spend 28–50% of their time traveling, presumably in search of prey (Peterson et al. 1984, Mech 1992), so preferential use of landscape features that improve movement efficiency should be beneficial. At the disturbed site, where road density was high (0.53 linear km/km²), wolves showed a weak bias toward these features. Use of the few existing anthropogenic corridors was not observed at the undisturbed site possibly due to their limited availability (Fig. 1). Instead, in the absence of...
widespread anthropogenic features, frozen lakes
were strongly selected.

Wolves showed avoidance of areas with abundant caribou or preferred caribou habitat. Caribou
have been shown to space out or away from
concentrated wolf travel routes (Bergerud et al. 1984, Dussault et al. 2012) and isolate themselves from
other more abundant primary prey species and
their shared predators to reduce negative effects
of predation (Bergerud and Page 1987, Seip 1992). Interestingly, in our study area, caribou avoided
moose habitat more strongly than they avoided
wolves (Avgar et al. 2015). Our findings thus
support the notion that caribou predation by
wolves is incidental, as wolves clearly concentrate
their space use in areas of high-quality moose
habitat and hence away from caribou.

Spatial scale can exert a strong influence on
resource-use patterns (Boyce 2006). Here, we
investigated resource utilization at a large extent
(>20,000 km²) and coarse resolution (25 km²)
allowing observation and identification of
broad-scale patterns of wolf behavior. Directly
informed landscape-scale studies such as ours
are rare and provide compelling evidence about
the population-level spatial behaviors that

Table 4. Comparison of variable coefficient estimates across all models showing 95% confidence intervals (CIs).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Variable</th>
<th>Model</th>
<th>0</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>PREY</td>
<td>0.0245979</td>
<td>(0.01092, 0.03828)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>0.0199766</td>
<td>(0.00616, 0.03379)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.0232647</td>
<td>(0.00948, 0.03705)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.0197309</td>
<td>(0.00589, 0.03357)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY</td>
<td>-0.0032137</td>
<td>(-0.00656, -0.00077)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>-0.0023786</td>
<td>(-0.00484, 0.00008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>-0.0030705</td>
<td>(-0.00551, -0.00063)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>-0.0023473</td>
<td>(-0.00481, 0.00012)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HABITAT</td>
<td>0.1001624</td>
<td>(0.03886, 0.16147)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>0.0845796</td>
<td>(0.02298, 0.14678)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.0975948</td>
<td>(0.03643, 0.15948)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.0836284</td>
<td>(0.02154, 0.14572)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HABITAT</td>
<td>0.0793161</td>
<td>(0.04223, 0.11683)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>0.1065460</td>
<td>(0.02751, 0.13041)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.0741114</td>
<td>(0.03438, 0.11385)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.0620624</td>
<td>(0.02191, 0.10221)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MOBILITY</td>
<td>0.0000178</td>
<td>(0.00000, 0.00035)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HABITAT + MOBILITY</td>
<td>0.0000667</td>
<td>(-0.00001, 0.00024)</td>
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<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.0001122</td>
<td>(-0.00006, 0.00029)</td>
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<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.0000451</td>
<td>(-0.00013, 0.00022)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Primary road density</td>
<td>0.1880435</td>
<td>(0.06696, 0.30913)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>0.1762104</td>
<td>(0.05454, 0.29788)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.1658574</td>
<td>(0.04455, 0.28176)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.1599171</td>
<td>(0.03815, 0.28168)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deciduous/mixed forest</td>
<td>0.1800435</td>
<td>(0.06696, 0.30913)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sparse forest</td>
<td>0.1762104</td>
<td>(0.05454, 0.29788)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Open water proportion</td>
<td>0.1800435</td>
<td>(0.06696, 0.30913)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + HABITAT</td>
<td>0.1599171</td>
<td>(0.03815, 0.28168)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PREY + MOBILITY</td>
<td>0.1452063</td>
<td>(0.03125, 0.25905)</td>
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<tr>
<td></td>
<td></td>
<td>PREY + HABITAT + MOBILITY</td>
<td>0.1402769</td>
<td>(0.03635, 0.24420)</td>
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<tr>
<td></td>
<td></td>
<td>Sparse forest</td>
<td>0.1503724</td>
<td>(0.03438, 0.26631)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Open water proportion</td>
<td>0.1503724</td>
<td>(0.03438, 0.26631)</td>
</tr>
</tbody>
</table>

Notes: Top overall models for each study area are highlighted. The response variable was the localized density distribution value transformed using a Box-Cox power transformation ($k = \frac{1}{4}$).
underlie ecosystem dynamics. However, as animal behavior is scale dependent, the full spectrum of animal–resource relationships is not observable in single-scale investigations (Kittle et al. 2008). For example, average moose density was 1.9 times higher and wolf density 1.6 times higher at the disturbed site than at the undisturbed site. This first-order-scale observation (Johnson 1980) is broadly consistent with the prey abundance hypothesis (Carbone and Gittleman 2002). At the smaller scale of the current analysis, wolves were selecting more consistently for the abundance of their prey’s resources than for the abundance of prey, suggesting hierarchical selection (McLoughlin et al. 2002). Therefore, although habitat selection patterns can be consistent across scales (Schaefer and Messier 1995, Prokopenko et al. 2016), they typically are not, allowing the possibility that wolves in our study area were selecting for prey abundance at a finer scale than our analysis investigated (McPhee et al. 2012b, but see Courbin et al. 2014). That wolf home range size is responsive to preferred prey abundance across the study area further suggests multi-scale selection (Kittle et al. 2015).

The novel methods employed in this study included amalgamating multiple pack-level UDs, weighted by pack size to create annual winter population-level LDDs. These were then combined to develop a multi-pack, multi-year amalgamated LDD. An advantage of amalgamating space-use data in this way instead of inferring population-level processes by averaging un-standardized coefficients from individual-level resource utilization functions (e.g., Marzluff et al. 2004, Long et al. 2009) is that landscape-level spatial patterns were directly informed from telemetry relocations, and not inferred from a more restricted area of observation. Another advantage of this amalgamation method is that it allows the individual differences typically arising from the state (i.e., pregnant, hungry), circumstance (e.g., post-pack split), or unique individual behavioral characteristics of animals within a population, to be incorporated into model structure but still synthesized so that selection processes driving the observed broad-scale patterns can be detected. In contrast, when investigating selection processes at the group level, a general synthesis of broad-scale space-use patterns is less likely due to the wide range of group-specific influential factors detected (Bowler and Benton 2005). Weighting individual UDs by group size emphasizes selection patterns of large groups, thereby properly reflecting population-level use, but is equally valuable in buffering the effect, without discounting it, of satellite individuals (i.e., group size =1) whose spatial behavior, which nevertheless influences observed population-level patterns (Bolnick et al. 2003, Araujo et al. 2011), is typically underlain by motivations at variance with any potential population norms. Therefore, amalgamation of individual packs and weighting by group size should provide a more accurate reflection of the landscape utilization by the larger population than would have a pack-by-pack analysis or unweighted amalgamation.

The present study was able to utilize an unusually large data set with dozens of individuals representing numerous social groups over multiple years. Although this did provide considerable analytical depth, the method is not restricted to use with such data-rich studies. Where fewer social groups are monitored and/or for a shorter duration, it is still possible to develop population-level LDDs from which meaningful inferences can be drawn (e.g., Kittle et al. 2016). An important caveat here is that the influence of group-level variation in spatial behavior on observed patterns should be inversely correlated with the number of groups monitored.

Since the logic underlying the current method calls for monitored groups to define space use at a population level, the presence of un-monitored groups on the same landscape is potentially problematic, especially if they spatially overlap the study animals. The present method addresses this issue in multiple ways. First, by focusing on groups with little spatial overlap (i.e., territorial species), the probability of an un-monitored group extensively using the same space as a monitored group is greatly reduced. Furthermore, existing areas of overlap are restricted to peripheral parts of the range allowing the presence of un-monitored groups to be detected as “holes” in the amalgamated layer. These potential “holes” do not unduly influence the population-level LDD because they are left out of it. Secondly, by dividing the cumulative use value of each cell on the landscape by the number of years for which data were available for that cell, we can further minimize the bias of un-monitored groups such that if a LDD cell value comes from a group
monitored in only one of three possible years, the
value of the cell is divided by 1 when creating the
final cumulative LDD. A bias remains where a
peripheral part of a monitored group's range
(with a presumably low use value), either at the
edge of the study area or adjacent to a “hole,” is
likely to be overlapped by the peripheral part of
another, un-monitored group’s range. Here, the
overall “wolf-use” value of that cell would be
underrepresented. The present method attempts
to minimize this potential bias by trimming cell
values <0.05 from the cumulative LDD, effectively
removing most of these potentially biased cells.

Although we have focused here on explicitly
group-living species, there is no reason that this
method cannot be expanded to investigate space-
use patterns of more solitary species assuming
similar spatial configuration of ranges. Under
this scenario, when group size is one, the end
product of the amalgamation process could
legitimately be called a population-level UD
(Jennrich and Turner 1969).

In summary, using this promising new method-
ological approach to understanding social carnio-
vore space use, we see some support for each of
the three hypotheses tested, indicating that
wolves may use a combination of strategies to
increase encounter rate with their prey when
moving through the landscape, reflective of local
ecological conditions. The most consistent result
was strong use by wolves of areas where moose
forage was abundant, suggesting that wolves pri-
marily selected to exploit their preferred prey
indirectly by using spatially predictable patches
of this prey’s preferred habitat. How wolves sup-
plement this strategy appears to depend on prey
density, with wolves targeting prey directly where
density is high enough to make this profitable
and disproportionately utilizing landscape fea-
tures that promote mobility where low prey den-
sity makes direct tracking of prey unprofitable.

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LITERATURE CITED

Anderson, M. 2012. Wolf responses to spatial variation
University of Guelph, Guelph, Ontario, Canada.

The ecological causes of individual specialization.

rates of diffusion and consumption in relation to

Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell.
2013. Environmental and individual drivers of ani-
mal movement patterns across a wide geographical

Avgar, T., et al. 2015. Space-use behaviour of wood-
land caribou based on a cognitive movement

Bednekoff, P. A. 2007. Prehistory: before foraging met
danger. Pages 6–8 in D. W. Stephens, J. S. Brown,
and R. C. Ydenberg, editors. Foraging: behavior
and ecology. The University of Chicago Press,
Chicago, Illinois, USA.

Belovsky, G. E. 1981. Optimal activity times and

competition with wolves limit the distribution and
abundance of coyotes? Journal of Animal Ecology
76:1075–85.

Antipredator tactics of calving caribou: dispersion
in mountains. Canadian Journal of Zoology 62:
1566–1575.

and dispersion of parturient caribou at calving as
antipredator tactics. Canadian Journal of Zoology
65:1597–1606.

(Version 0.7.2.1). http://www.spatalecology.com/
gme

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang,
The ecology of individuals: incidence and implica-
tions of individual specialization. American Natu-

sequences of animal dispersal strategies: relating
individual behavior to spatial dynamics. Biological
Reviews 80:205–225.

Boyce, M. S. 2006. Scale for resource selection func-

Brown, G. S. 2011. Patterns and causes of demographic
variation in a harvested moose population: evidence
for the effects of climate and density-dependent


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