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). Termed "leap-frogging" (Sih 2005), the 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
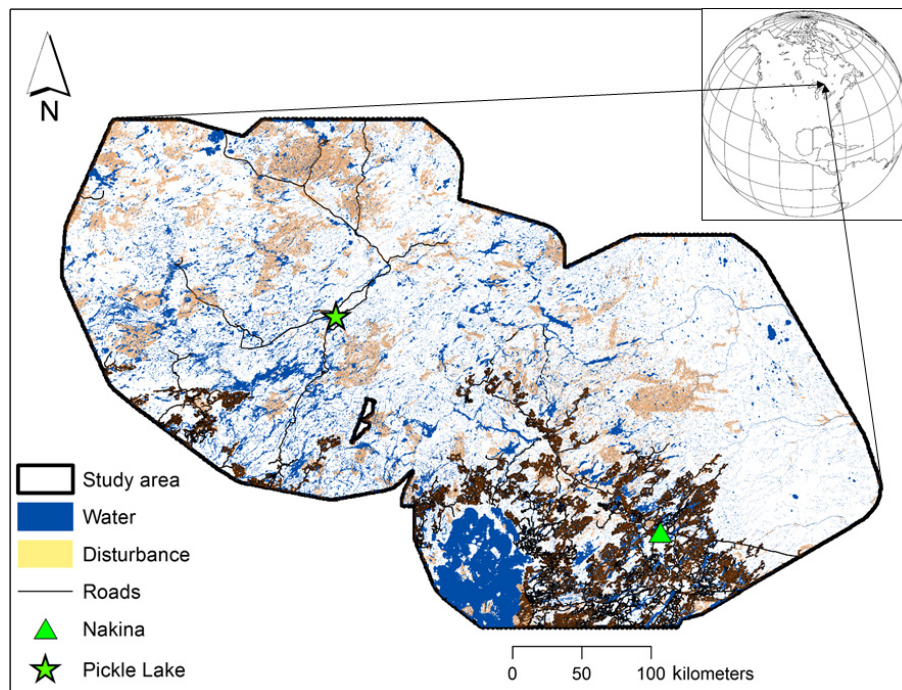
Fig. 1. Study area location within North America (inset). Road networks, both primary (paved and maintained) and tertiary (unpaved, not maintained), are shown. Note heavily concentrated roads in the disturbed southeast section (Nakina) and sparse network in the undisturbed northwest section (Pickle Lake). Pale brown areas on the landscape represent disturbance from fire and forestry. Note smaller, more widespread, anthropogenic disturbance in southeast (Nakina) and large, clumped disturbance (from three large fires) in northwest (Pickle Lake). White patch with sharp, straight lines in approximate middle of image is cloud cover that obscured satellite imagery.

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 UDs (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 UDs (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 UDs 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.
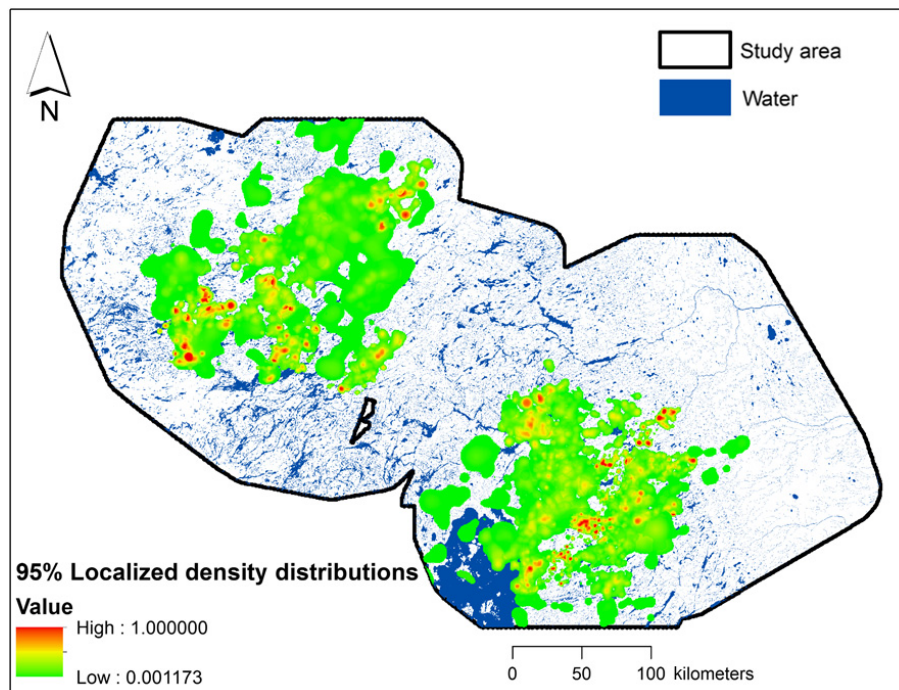
Fig. 2. Landscape-level 95% winter localized density distributions for wolf packs in the undisturbed northwest (Pickle Lake) and disturbed southeast (Nakina) sites within the study area. Eleven wolf packs and two satellite individuals encompassing 9034 telemetry relocations were used to determine the 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.

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

Table 1. Full models inclusive of all potential predictor variables for each of three hypotheses.

Hypothesis	Variable	Definition
Prey abundance	Relative moose density	Moose/km^2/pixel
	Caribou relocations	Telemetry relocations/season/pixel
Prey habitat	Deciduous/mixed upland	Pixel proportion (deciduous treed + mixed treed classes)
	Sparse treed	Pixel proportion (sparse treed class)
	Coniferous treed	Pixel proportion (coniferous treed class)
	Disturbed	Pixel proportion (disturbed (non-treed) + disturbed (treed) classes)
Predator mobility	Primary roads	Meters/pixel (includes paved as well as maintained gravel)
	Tertiary roads	Meters/pixel (unpaved roads and utility lines; un-maintained)
	Linear water	Meters/pixel (shorelines including lakes and rivers)
	Frozen waterbodies	Pixel proportion (clear open water + turbid water classes)

Notes: A backward stepwise procedure using likelihood ratio tests was conducted to reduce these full models to the top models for each hypothesis. The response variable was the localized density distribution value transformed using a Box–Cox power transformation ($\lambda = \frac{1}{4}$).

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-m² resolution, and moose abundance, measured at a 25-km² 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-km²) 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 (w_i) 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 w_i 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 2. Model-averaged coefficient estimates (θ) with unbiased standard errors (SE).

Study area	Model	Variable	θ	SE
Nakina	PREY	Moose density††	0.019934	0.007060
		Caribou relocations†	−0.002375	0.001258
	HABITAT	Deciduous/mixed forest††	0.085006	0.031716
		Disturbed††	0.064897	0.019880
	MOBILITY	Primary road density	0.000047	0.000089
Pickle Lake	PREY	Caribou relocations	−0.001549	0.001414
	HABITAT	Deciduous/mixed forest††	0.163640	0.062072
		Sparse forest	−0.192980	0.127653
	MOBILITY	Open water proportion††	0.016353	0.004709

Note: The response variable was the localized density distribution value transformed using a Box–Cox power transformation ($\lambda = \frac{1}{4}$).

†/†† 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 ΔAIC 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_i 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_i 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 ΔAIC, Akaike weights (w_i), and relative rank.

Model	Nakina			Pickle Lake		
	ΔAIC	w_i	Rank	ΔAIC	w_i	Rank
PREY	10.339	0.004	5	19.119	0.000	7
HABITAT	6.839	0.022	3	10.533	0.003	6
MOBILITY	21.856	0.000	7	6.366	0.024	3
PREY + HABITAT	**0.000**	**0.676**	**1**	9.379	0.005	5
HABITAT + MOBILITY	8.250	0.011	4	**0.000**	**0.569**	**1**
PREY + MOBILITY	10.696	0.003	6	6.402	0.023	4
PREY + HABITAT + MOBILITY	1.734	0.284	2	0.829	0.376	2
NULL	24.308	0.000	8	21.430	0.000	8

Notes: AIC, Akaike's information criterion. Top models for each study site are highlighted.
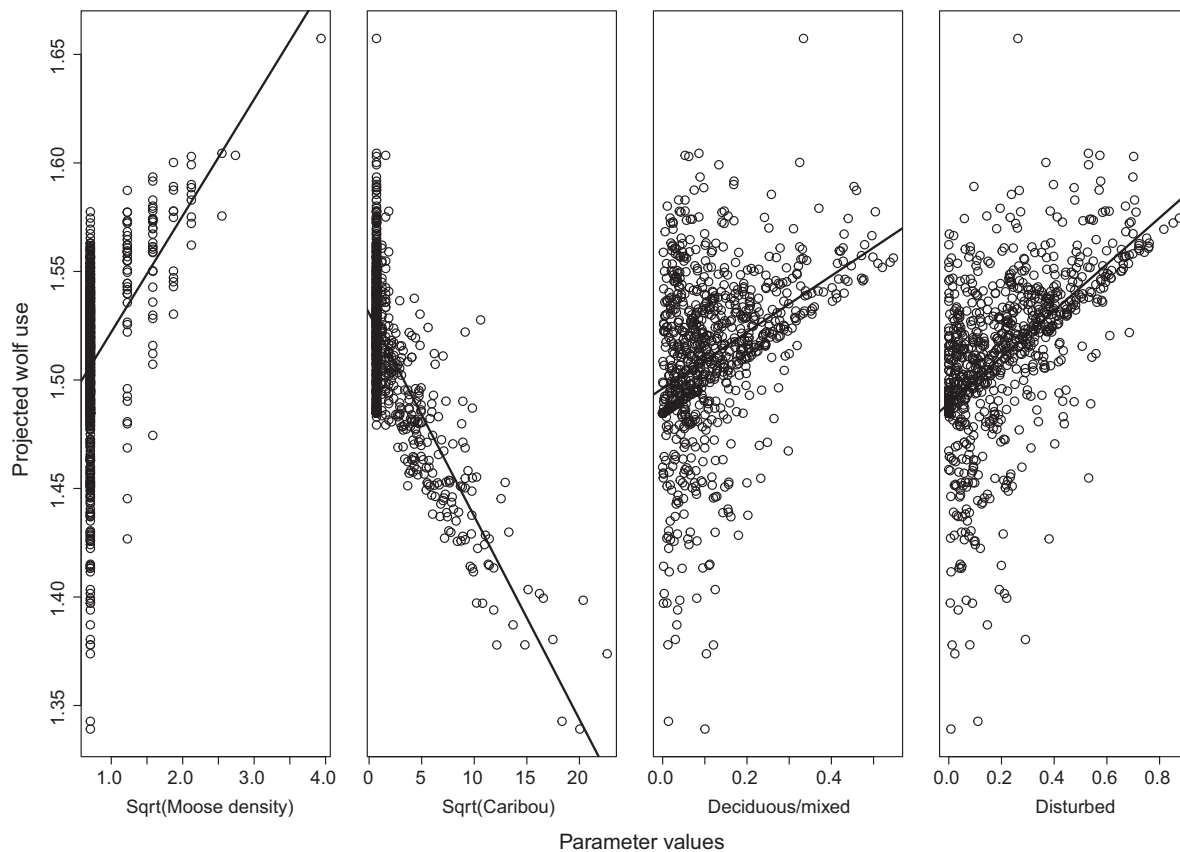
Fig. 3. Sensitivity analysis of input variables comprising the best wolf space-use model at Nakina. The far left graph shows localized density distribution values projected from the top Nakina model (PREY + HABITAT) against the square root of moose density input variable values (Pearson's correlation $|r| = 0.43$). 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 ($P < 0.0001$).

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
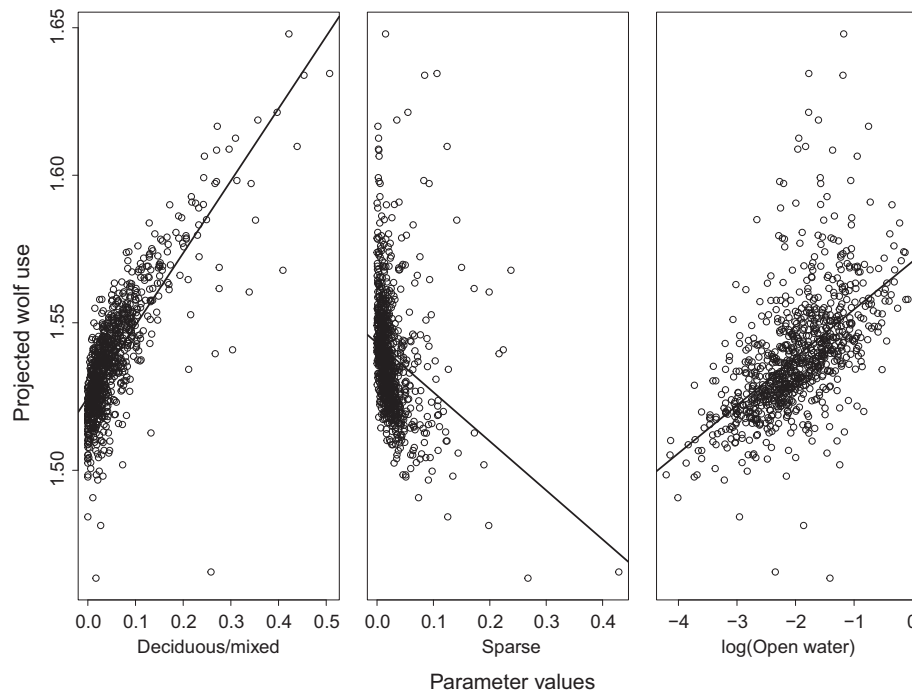
Fig. 4. Sensitivity analysis of input variables comprising the best wolf space-use model at Pickle Lake. The left graph shows localized density distribution values projected from the top Pickle Lake model (HABITAT + MOBILITY) against the proportion of deciduous/mixed forest input variable values (Pearson's correlation $|r| = 0.78$). The middle graph shows the same model output on the y-axis against the proportion of sparse forest input variable values ($|r| = -0.27$). The right graph shows the same model output on the y-axis against log of the proportion of open water input variable value ($|r| = 0.56$). Both the visual pattern and the Pearson's correlation coefficients indicate that the proportion of deciduous/mixed forest is the more influential variable. All correlations are significant ($P < 0.0001$).

rules, and consistent with foraging models allowing predators and prey to move and respond to each other's movement (Mitchell and Lima 2002). 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
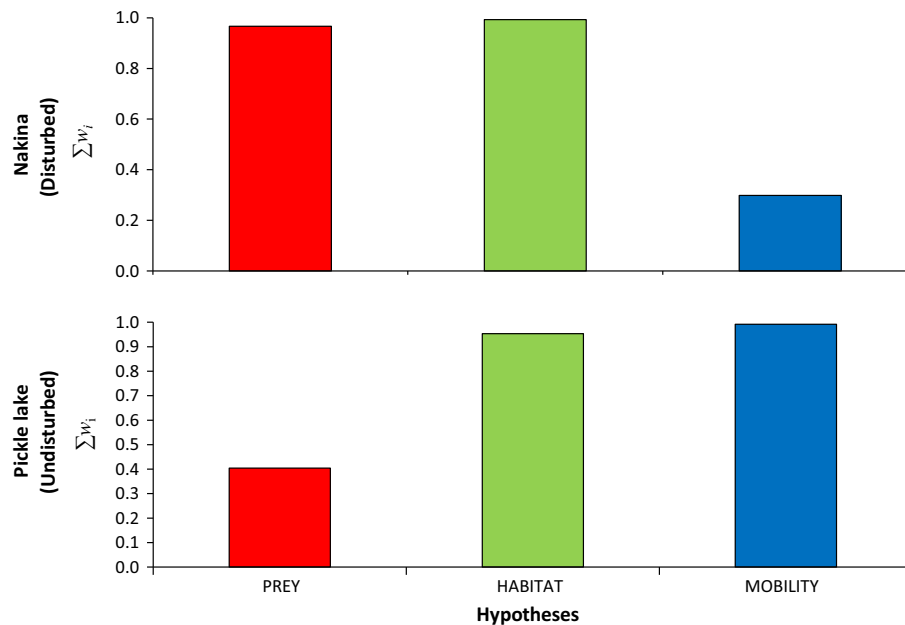
Fig. 5. Comparison of summed Akaike weights (w_i) for prey abundance (PREY), prey resources (HABITAT), and predator mobility (MOBILITY) model variables in both study areas. Weights are from all models within the full model set that incorporate each variable class. Each is represented four times in full model set allowing direct comparison.

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 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

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

Study area	Variable	Model	θ	95% CI
Nakina	Moose density	PREY	0.0245979	(0.01092, 0.03828)
		PREY + HABITAT	**0.0199766**	**(0.00616, 0.03379)**
		PREY + MOBILITY	0.0232647	(0.00948, 0.03705)
		PREY + HABITAT + MOBILITY	0.0197309	(0.00589, 0.03357)
	Caribou relocations	PREY	−0.0032137	(−0.00565, −0.00077)
		PREY + HABITAT	**−0.0023786**	**(−0.00484, 0.00008)**
		PREY + MOBILITY	−0.0030705	(−0.00551, −0.00063)
		PREY + HABITAT + MOBILITY	−0.0023473	(−0.00481, 0.00012)
	Deciduous/mixed forest	HABITAT	0.1001624	(0.03886, 0.16147)
		PREY + HABITAT	**0.0848796**	**(0.02298, 0.14678)**
		HABITAT + MOBILITY	0.0979548	(0.03643, 0.15948)
		PREY + HABITAT + MOBILITY	0.0836284	(0.02154, 0.14572)
	Disturbed forest	HABITAT	0.0795316	(0.04223, 0.11683)
		PREY + HABITAT	**0.0654604**	**(0.02751, 0.10341)**
		HABITAT + MOBILITY	0.0741114	(0.03438, 0.11385)
		PREY + HABITAT + MOBILITY	0.0620624	(0.02191, 0.10221)
	Primary road density	MOBILITY	0.0001798	(0.00001, 0.00035)
		HABITAT + MOBILITY	0.0000687	(−0.00011, 0.00024)
		PREY + MOBILITY	0.0001122	(−0.00006, 0.00028)
		PREY + HABITAT + MOBILITY	0.0000451	(−0.00013, 0.00022)
Pickle Lake	Caribou relocations	PREY	−0.0019964	(−0.00387, −0.00013)
		PREY + HABITAT	−0.0025038	(−0.00527, 0.00026)
		PREY + MOBILITY	−0.0013576	(−0.00325, 0.00053)
		PREY + HABITAT + MOBILITY	−0.0015479	(−0.00436, 0.00127)
	Deciduous/mixed forest	HABITAT	0.1880435	(0.06696, 0.30913)
		PREY + HABITAT	0.1762104	(0.05454, 0.29788)
		HABITAT + MOBILITY	**0.1658574**	**(0.04455, 0.28716)**
		PREY + HABITAT + MOBILITY	0.159917	(0.03815, 0.28168)
	Sparse forest	HABITAT	−0.262498	(−0.51037, −0.01463)
		PREY + HABITAT	−0.2347696	(−0.48434, 0.01480)
		HABITAT + MOBILITY	**−0.1975932**	**(−0.44688, 0.05169)**
		PREY + HABITAT + MOBILITY	−0.1848719	(−0.43528, 0.06553)
	Open water proportion	MOBILITY	0.0192596	(0.01026, 0.02825)
		HABITAT + MOBILITY	**0.0166572**	**(0.00761, 0.02570)**
		PREY + MOBILITY	0.0180997	(0.00901, 0.02719)
		PREY + HABITAT + MOBILITY	0.0156025	(0.00636, 0.02485)

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 ($\lambda = \frac{1}{4}$).

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

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, Araújo 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 methodological approach to understanding social carnivore 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 primarily selected to exploit their preferred prey indirectly by using spatially predictable patches of this prey's preferred habitat. How wolves supplement 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 features that promote mobility where low prey density makes direct tracking of prey unprofitable.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1783/full