







ARTICLE

Resource exploitation efficiency collapses the home range of an apex predator

Melanie Dickie^{1,2}  | Robert Serrouya¹  | Tal Avgar³  | Philip McLoughlin⁴ |
 R. Scott McNay⁵ | Craig DeMars¹  | Stan Boutin⁶  | Adam T. Ford² 

¹Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada

²Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada

³Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah, USA

⁴Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

⁵Wildlife Infometrics, Mackenzie, British Columbia, Canada

⁶Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Correspondence

Melanie Dickie

Email: mvezina@ualberta.ca

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Abstract

Optimizing energy acquisition and expenditure is a fundamental trade-off for consumers, strikingly reflected in how mobile organisms use space. Several studies have established that home range size decreases as resource density increases, but the balance of costs and benefits associated with exploiting a given resource density is unclear. We evaluate how the ability of consumers to exploit their resources through movement (termed “resource exploitation”) interacts with resource density to influence home range size. We then contrast two hypotheses to evaluate how resource exploitation influences home range size across a vast gradient of productivity and density of human-created linear features (roads and seismic lines) that are known to facilitate animal movements. Under the Diffusion Facilitation Hypothesis, linear features are predicted to lead to more diffuse space use and larger home ranges. Under the Exploitation Efficiency Hypothesis, linear features are predicted to increase foraging efficiency, resulting in less space being required to meet energetic demands and therefore smaller home ranges. Using GPS telemetry data from 142 wolves (*Canis lupus*) distributed over more than 500,000 km², we found that wolf home range size was influenced by the interaction between resource density and exploitation efficiency. Home range size decreased as linear feature density increased, supporting the Exploitation Efficiency Hypothesis. However, the effect of linear features on home range size diminished in more productive areas, suggesting that exploitation efficiency is of greater importance when resource density is low. These results suggest that smaller home ranges will occur where both linear feature density and primary productivity are higher, thereby increasing regional wolf density.

KEYWORDS

Canis lupus, foraging, home range, linear features, resource availability, resource exploitation

INTRODUCTION

Maximizing energy acquisition while minimizing energy expenditure is a fundamental trade-off faced by all

organisms (Charnov, 1976). For mobile organisms, foraging theory centers around the behavioral decisions animals make to optimize this energetic trade-off, including the effort spent on searching for and exploiting resources,

exposure to predation risk, and diet preferences (Brown, 1999; Pyke et al., 1977). These behavioral decisions can scale up into patterns of distribution and abundance for both consumers and resources (Fretwell & Lucas, 1969). Hence, the manner in which animals use space offers an information-rich paradigm through which we can understand aspects that limit the abundance of organisms.

A key process that links individual movement to the abundance and distribution of species is the formation and maintenance of home ranges, that is, the space used to meet life-history requirements (Burt, 1943). Home range size ties space use to regional density through the “packing” of home ranges (Wang & Grimm, 2007). Much like trade-offs consumers face while foraging, the size of a home range reflects a trade-off between the costs and benefits associated with acquiring resources, such as food and mates, over a given period of time (McNab, 1963). For species that defend a portion of the home range, termed a territory, the benefit of exclusive use of resources is balanced with the costs of defensive behaviors and aggressive interactions (Brown, 1964; Cubaynes et al., 2014). As such, territorial animals are expected to defend a home range large enough to meet their needs, but no larger (Calsbeek & Sinervo, 2002). For both territorial and non-territorial species, one key extrinsic determinant of home range size is forage resource availability, with home range size decreasing in more productive environments (Kodric-Brown & Brown, 1978; Snider et al., 2021).

While resource availability is often considered synonymous with resource density, availability is also related to the consumer’s ability to exploit those resources through movement (here termed “resource exploitation”; Pyke et al., 1977). Satiating processes can also decouple changes in resource density with changes in consumption rates, further complicating how resource density and exploitation influence home ranges. When resource density is low, resource exploitation likely becomes increasingly important for determining encounter and consumption rates, whereas when resource density is high, handling time can impose an increasingly large influence on consumption rates (Holling, 1959a). Despite the well-known inverse relationship between resource density and home range size, it is unclear how resource density and exploitation interact to influence home range formation and maintenance.

Resource exploitation is influenced by movement costs imposed by habitat heterogeneity and landscape permeability (Johnson et al., 1992). Despite the understanding that habitat heterogeneity can dramatically impact movement (Tucker et al., 2018), the link between movement costs and the formation and maintenance of

home ranges is unclear. Two hypotheses with opposing predictions can be invoked to predict how consumers will respond to variation in movement costs. Following marginal value theory, consumers in landscapes with low movement cost can reduce patch-residence times (Cowie, 1977; Ford, 1983), which leads to exploitation of additional patches. Consequently, travel between a greater number of patches leads to diffusive movements (Turchin, 1991) and the formation of large home ranges (Broadley et al., 2019), here termed the Diffusion Facilitation Hypothesis (Figure 1). However, following energetics theory, consumers in landscapes with low movement cost can instead expend less energy on traveling, and are therefore able to maintain a positive energy balance while exploiting lower resource density (Mitchell & Powell, 2004). A smaller area is therefore needed to maintain energetic demands, leading to the formation of small home ranges (Mitchell & Powell, 2004; Pyke et al., 1977), here termed the Exploitation Efficiency Hypothesis (Figure 1). The contrasting outcomes of how movement costs will affect home range size suggests that a more mechanistic understanding of resource exploitation is needed, particularly given the important consequences for understanding trophic interactions in changing landscapes (Lewis & Murray, 1993; Morales et al., 2010).

Anthropogenic habitat alteration has modified landscape permeability, having implications for the movement of many taxa across the globe (Tucker et al., 2018). In the boreal forest of North America, one of the most predominant forms of habitat alteration, particularly in western Canada, are linear features such as roads, seismic lines, or pipelines. Linear features facilitate the movement of predators like wolves (*Canis lupus*; Dickie et al., 2017, 2020), which is hypothesized to increase their encounter rates with prey, and thus kill rates (McKenzie et al., 2012). Increased wolf kill rates have important consequences for woodland caribou (*Rangifer tarandus*), which are in decline across much of their range as a result of increased predation (Serrouya et al., 2021; Wittmer et al., 2005). Although it is increasingly recognized that linear features are important for facilitating wolf movement (Dickie et al., 2017), how this process scales up to broad patterns of habitat use is unclear. Under the Diffusion Facilitation Hypothesis, increased movement efficiency from linear features would lead to diffusion and large home ranges. Conversely, under the Exploitation Facilitation Hypothesis, increased movement efficiency from linear features would increase foraging efficiency and lead to small home ranges. If linear features increase the ability of wolves to exploit a given density of resources, there may be a disconnect between resource density and “effective” resource density (i.e., the

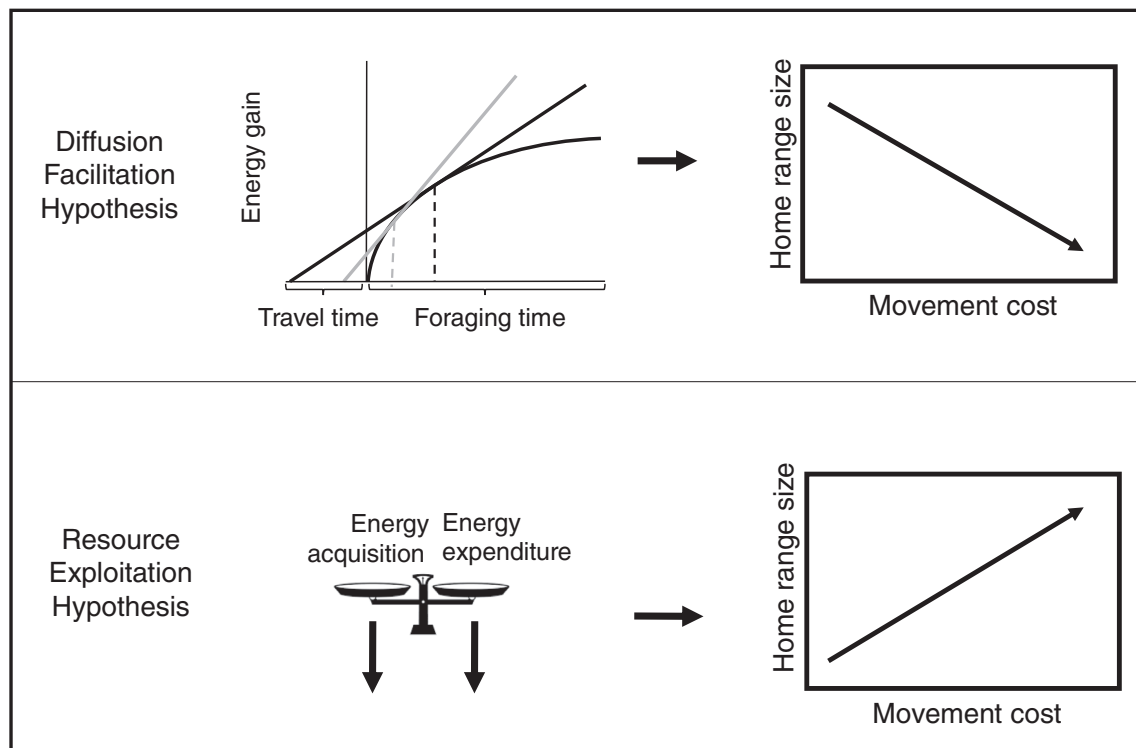


FIGURE 1 Conceptual diagram of how the Diffusion Facilitation Hypothesis and the Resource Exploitation Hypothesis make contrasting predictions of how movement cost influences home range size. Under the Diffusion Facilitation Hypothesis, consumers parse their time into interpatch travel (left of the solid arc), and intrapatch exploitation (right of the solid arc). Areas with lower movement cost (gray line) have lower inter-patch travel time compared to areas with higher movement cost (black line), and thus the optimal time to leave a patch (dashed lines) is shorter. Consumers that spend less time traveling between patches leave patches earlier, leading to more diffuse movements. Therefore, home range size is negatively correlated with movement cost. Under the Resource Exploitation Hypothesis, areas with less costly movement confer lower energy expenditure, and require less energy acquisition to maintain positive energy balances. In areas with lower movement cost, consumers can expend less energy to survive, and are thus able to forage in smaller areas. Therefore, home range size is positively correlated with movement cost

resource density a forager is successfully able to exploit in a given time and space).

In this study, we explore how resource density and exploitation combine to affect the home range size of wolves. First, we evaluate if home range area (i.e., a metric of size) is best explained by primary productivity (i.e., a metric of resource density), linear feature density (i.e., a metric of landscape capacity for resource exploitation), or the interaction between productivity and linear feature density. We predicted that the effect of resource exploitation on home range size is dependent on resource density, such that increased access to resources becomes more important when resource density is low. Next, we evaluate how resource exploitation affects home range size of wolves (Figure 1). If higher linear feature density facilitates diffusion across more resource patches (Diffusion Facilitation Hypothesis), we predict a positive relationship between home range area and linear feature density. Conversely, if higher linear feature density decreases the energy required to maintain a positive

energy balance (Exploitation Efficiency Hypothesis), we predict a negative relationship between home range area and linear feature density. We contrast the support for these hypotheses using data from 142 Global Positioning System (GPS)-collared wolves, distributed over more than 500,000 km², across a broad gradient of linear feature density and primary productivity.

METHODS

Study area

We used GPS location data collected from previous research programs located across four subregions of northwestern Canada: northeastern British Columbia (BC), northern Alberta (AB N), northeastern Alberta (AB NE), and Saskatchewan (SK; Figure 2). The study area spanned ecoregions of the Boreal Plains and Shield, as well as the Taiga Plains and Shield, and is represented

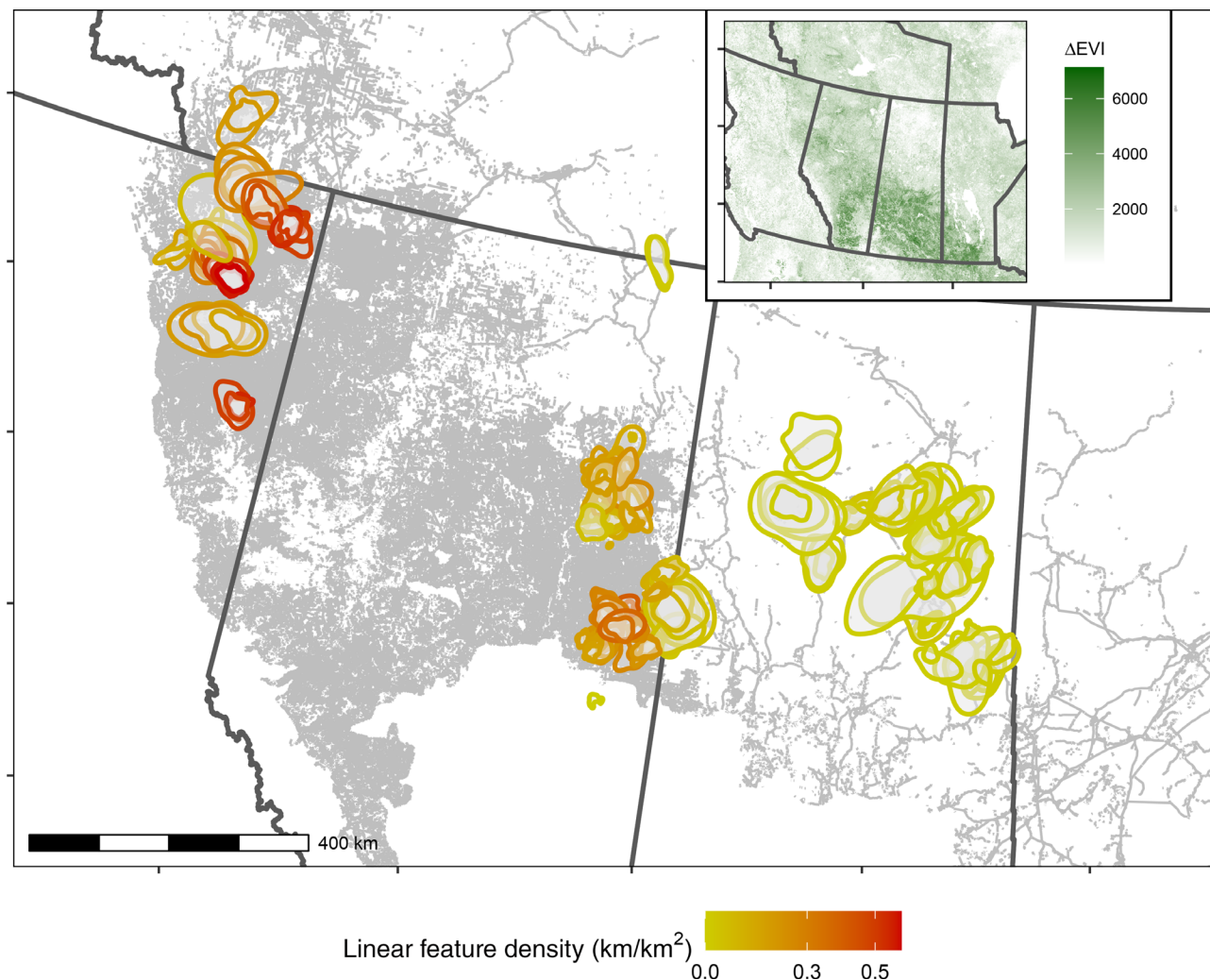


FIGURE 2 Seasonal wolf home ranges, estimated using 95% autocorrelated kernel density estimators, across a range of linear feature density (km/km^2) and primary productivity (ΔEVI [Enhanced Vegetation Index]) in northwestern Canada. Gray lines represent linear features within the boreal forest, and wolf home ranges are colored to represent the surrounding linear feature density within each home range. Data were collected from 36 individuals in British Columbia, 34 individuals from northern Alberta, 44 individuals from northeastern Alberta, and 28 individuals from Saskatchewan. The inset map depicts the productivity gradient (ΔEVI) across the study area, calculated as the median EVI in the 2020 leaf-on season minus the median EVI value in the 2020 leaf-off season. Black lines represent the provinces and territories of Canada

by a mosaic of uplands and peatlands (Appendix S1). Forest cover is predominantly coniferous (black spruce *Picea mariana*, white spruce *Picea glauca*, jack pine *Pinus banksiana*, and tamarack *Larix laricina*), with some deciduous and mixedwood forest (trembling aspen *Populus tremuloides*, white birch *Betula papyrifera*, and balsam poplar *Populus balsamifera*). The Boreal and Taiga Shield are represented by wetter, less productive habitat and shorter fire return intervals than the Boreal and Taiga Plains. The study area is undergoing anthropogenic habitat alteration via the cutting of forests for timber and oil and gas exploration (Alberta Biodiversity Monitoring Institute, 2018), and the conversion of forests to agriculture (Hobson et al., 2002). Population density within the study area was below 1 person/ km^2 .

Subregions varied between 0.1 and 0.8 people/ km^2 (Statistics Canada, 2017). Additional information about the habitat and human use of the study area are provided in Appendix S1.

Quantifying home range size

GPS telemetry data were collected between 2011 and 2017 from 36 individuals in 15 packs (BC), 34 individuals from 10 packs (AB N), 44 individuals from 16 packs (AB NE), and 28 individuals from 19 packs (SK). Animals were captured and handled with approved Animal Care under the University of Alberta (AUP00000480, AUP00000040, AUP00000102, AUP000001309) or

University of Saskatchewan (AUP20130127). One to seven individuals were monitored per pack per year, with a median of two individuals. Collars were programmed to retrieve GPS locations at varying intervals, from 5 min to 3 h. We visually checked for location errors, and rarified data to the largest interval between fixes (i.e., 3-h locations). Because individuals may shift their home ranges across seasons, we divided data into two seasons, roughly corresponding to the snow (November–April) and snow-free (May–October) seasons.

We were unable to delineate the defended and undefended portion of the home range to quantify territory size. We therefore opted to evaluate wolf “home range” size as per Ciucci et al. (1997); Mancinelli et al. (2018); and Mattisson et al. (2013), while recognizing that a portion of the home range is defended. To quantify home range area, we created 95% autocorrelated kernel density estimators (aKDEs; Fleming et al., 2015; Noonan et al., 2019) for each individual in each season using the *ctmm* package in R (Calabrese et al., 2016). Prior to creating aKDEs, we removed any individual season combination with fewer than 50 locations and visually assessed and removed individual seasons with extra-territorial forays. As suggested by Calabrese et al. (2016), we used Maximum Likelihood to fit independent identically distributed, Brownian motion, Ornstein–Uhlenbeck, integrated Ornstein–Uhlenbeck, and Ornstein–Uhlenbeck Foraging models, and selected the model with the lowest Akaike Information Criterion (AIC) score (Akaike, 1974). The number of seasonal individual home ranges per study subregion, year, and season are presented in Appendix S1: Table S1.

Environmental attributes

We quantified environmental attributes available in each individual’s seasonal home range. To represent the area in which individuals defined their home range, we buffered the centroid of each seasonal home range by the average radius of seasonal home ranges (mean = 50 km). We calculated the density of linear features within each of these buffered centroids using a publicly available data set of disturbances (Environment and Climate Change Canada, 2012). This data set uses LANDSAT imagery at a 30-m cell size, which may under-estimate the density of linear features that are typically smaller than this cell size. However, these data are consistently collected across boreal Canada to allow comparisons across study subregions.

Increased moose (*Alces alces*) density has been associated with increased wolf density (Fuller, 1989; Serrouya et al., 2021). However, in the absence of robust prey

density estimates within each study subregion, we used primary productivity as a surrogate for resource density. Remote-sensing indicators of primary productivity have been shown to represent habitat quality for ungulates (Street et al., 2015). We used the change in the Enhanced Vegetation Index (EVI) as a metric of primary productivity, and assumed that this metric was related to wolf prey density (Bergerud & Elliot, 1986; Street et al., 2015). We tested our assumption that primary productivity is an appropriate index of wolf prey density by evaluating the relationship between moose density and primary productivity in a sub-analysis (Figure 3; see Appendix S2 for methodological details).

We extracted EVI using the MODIS Terra Vegetation Indices 16-Day Global, with a 500 m cell size. For each year the median EVI value from the leaf-on (1 July–1 August) and leaf-off (1 September–1 October) were extracted as measures of productivity at peak vegetation growth, and when deciduous vegetation has died back, but before snow falls, respectively. The leaf-off median EVI was subtracted from the leaf-on median EVI to calculate the change in EVI (Δ EVI). To remove pixels covered by clouds or shadows we retained only pixels classified as “VI produced, good quality.” Pixels covered by water were removed following Hansen et al. (2013).

Analytical framework

To test if wolf seasonal home range area was driven by resource density, resource exploitation, or the interaction, we compared the support for models including linear feature density only, Δ EVI only, or the interaction of linear feature density and Δ EVI in a model comparison framework using Akaike’s Information Criterion (AIC; Akaike, 1974). First, we determined the random effects structure to account for non-independence between multiple seasonal home ranges from the same individual and individuals in the same pack. We included all fixed effects and discriminated against animal as a random intercept, animal and pack as random intercepts, and animal nested within pack as a random intercept using Restricted Maximum Likelihood (Zuur et al., 2009). We then incorporated the random intercept structure with the lowest AIC in subsequent model selection. We additionally tested the additive effect of linear feature density and primary productivity to understand if the interaction effect was spurious.

To account for unmeasured differences across the four sub-study regions, as well as differences among years and between the snow and snow-free season, we discriminated between models including fixed effects and interactions for study region, season using Maximum Likelihood (Zuur et al., 2009). We included the

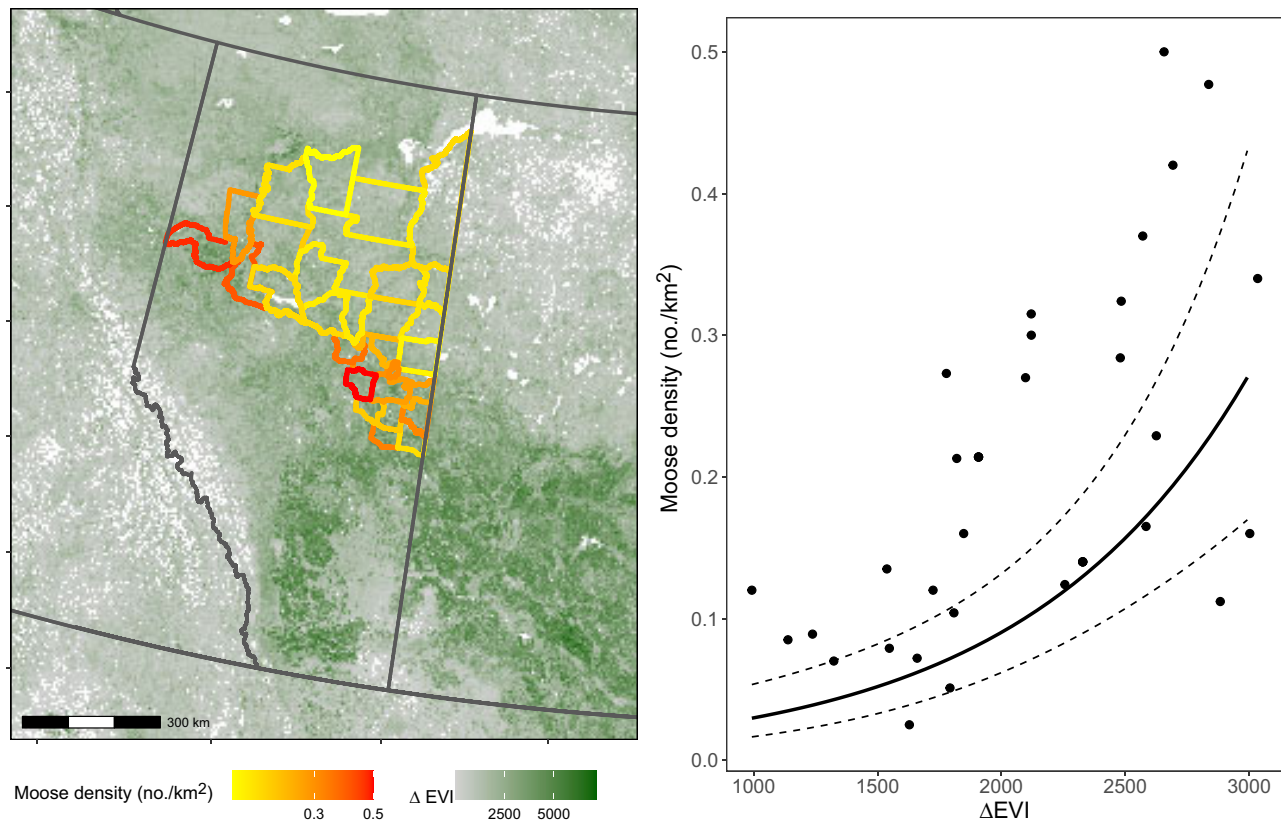


FIGURE 3 (a) Moose densities (no./km²) across a primary productivity (ΔEVI [Enhanced Vegetation Index]) gradient in northern Alberta (AB N). Boundaries of the moose survey areas are colored to represent the estimated moose densities within each moose survey area from aerial surveys. The productivity gradient (ΔEVI) across the study area, calculated as the median EVI in the 2020 leaf-on season minus the median EVI value in the 2020 leaf-off season. Black lines represent the provinces and territories of Canada. (b) Estimated moose density (no./km²) as a function of primary productivity (average ΔEVI) within each moose survey area in AB N. The solid line represents the predicted relationship between moose density and ΔEVI while including year, survey method, and region as fixed effects and set at the reference conditions (year, 2014; method, distance sampling; region, boreal). Dashed lines represent 95% confidence intervals of the predicted relationship

monitoring period, defined as the number of days each individual was monitored, scaled between zero and one, as a fixed effect in all models to account for variation in the duration of monitoring. We then incorporated the basic fixed effects model structure with the lowest AIC in subsequent model selection to compare the support for models including linear feature density only, ΔEVI only, or the interaction of linear feature density and ΔEVI. We scaled ΔEVI between zero and one to place it on a similar scale to linear feature density, and scaled monitoring period between zero and one.

Finally, to compare the support for the Diffusion Facilitation Hypothesis and Resource Exploitation Hypothesis we evaluated if there is a positive or negative slope, respectively, in the most supported model. We plotted the raw data and predicted response curves of home range size as a function of linear feature density and scaled ΔEVI using the most competitive models. We held other continuous variables constant at the mean,

and categorical fixed effects at the reference category. We evaluated the predictive capacity of the final model using leave-one-out (LOO) model validation (Zuur et al., 2009).

Pack size and sex

Previous research has shown that wolves adapt territory size, not pack size, to local resource density (Kittle et al., 2015; but see Messier & Crête, 1985). However, it is possible that smaller home range supports a lower pack size and does not result in a numerical response of wolf population size to prey density or exploitation efficiency. Furthermore, males and females typically differ in their home range size (Kodric-Brown & Brown, 1978). Sex and pack size (estimated as the minimum count of pack members) were estimated during captures but were not available for all individuals. Additionally, pack cohesion varies by season, and as such pack size at capture may

TABLE 1 The effect of linear feature density (km/km²), primary productivity (Δ EVI, scaled between 0 and 1), monitoring period (number of days monitored, scaled between 0 and 1), season (snow and snow free), and study subregion on seasonal wolf home range area (km²)

Coefficient	Estimate	−CI	+CI
Intercept	9.713	8.877	10.550
Monitoring period	0.431	0.221	0.640
Snow free	−0.463	−0.602	−0.324
AB NE	−1.114	−1.432	−0.796
SK	−1.352	−1.888	−0.817
AB N	−1.484	−1.844	−1.125
Linear feature density	−5.467	−9.403	−1.530
Δ EVI	−2.660	−3.824	−1.497
Linear feature density \times Δ EVI	5.704	−0.541	11.948

Notes: Home range area was calculated using 95% autocorrelated kernel density estimators and was log-transformed. Model estimates and 95% CIs are shown for mixed-effects models with pack-year included as a random intercept. The snow season and British Columbia are set as the reference categories. Abbreviations: AB N, northern Alberta; AB NE, northeastern Alberta; CI, confidence interval; EVI, Enhanced Vegetation Index; SK, Saskatchewan.

not necessarily reflect seasonal variation in pack sizes (Metz et al., 2011). For these two reasons, we used sub-analyses to test if our interpretations were sensitive to the effects of sex and pack size (Appendix S3), but did not incorporate sex and pack analyses into our primary analyses.

First, using only individuals where pack size and sex were estimated, we tested if including these variables lowered the AIC score of the top competing model above. Second, we modeled the residuals of the top competing model as a function of pack size and sex to evaluate if the discrepancy between predicted and observed home range area in our main analysis was influenced by these variables. We found no evidence that pack size or sex improved model fit or influenced the relationship between observed and predicted wolf seasonal home range area (Appendix S3).

Data accessibility

All data are available from Dryad <https://doi.org/10.5061/dryad.ns1rn8pth>. All code and data used for analyses are available from <https://doi.org/10.5281/zenodo.5643218>.

RESULTS

Primary productivity (Δ EVI) as an index of prey density

Average moose density increased by 1.12 times for every 100-unit increase in Δ EVI ($\beta = 0.001$, $SE \leq 0.001$, $p \leq 0.001$; Figure 3, Appendix S2: Table S1).

Wolf home range size

The top competing model included Δ EVI, linear feature density, and the interaction between Δ EVI and linear feature density, along with monitoring period, season, and study subregion as basic fixed effects, and pack-year as a random intercept (Appendix S4: Table S1). While the additive model of linear feature density and Δ EVI had similar support as the interaction model (Appendix S4: Table S1), we provide effect sizes based on the interaction model, which explicitly tests our hypothesis. See Appendix S4: Table S2 for effect sizes and model output for the additive model.

Seasonal wolf home range area significantly decreased as linear feature density and Δ EVI increased (Table 1, Figure 4). The effect of linear feature density diminished as Δ EVI increased (Figure 4). For example, when Δ EVI was at the lowest value observed, average wolf home ranges were approximately 2.7 times larger (snow: 21,211 km² to 7760 km²; snow-free: 13,354 km² to 4885 km²) as linear feature density increased from zero to the mean linear feature density (i.e., 0.18 km/km²). Comparatively, when Δ EVI was at its mean, the average wolf home range was only approximately 1.5 times larger (snow: 4878 km² to 3186 km²; snow-free: 3071 km² to 2006 km²) as linear feature density increased from zero to the mean linear feature density. Additionally, wolf home range size was significantly smaller, on average, in the snow-free season than the snow season, and increased with increasing monitoring period (Table 1).

Linear feature density and Δ EVI were correlated at 0.44. Nakagawa's conditional R^2 for the model was 0.73 and marginal R^2 was 0.40. The adjusted R^2 from LOO model validation was 0.35. On average observed seasonal home ranges

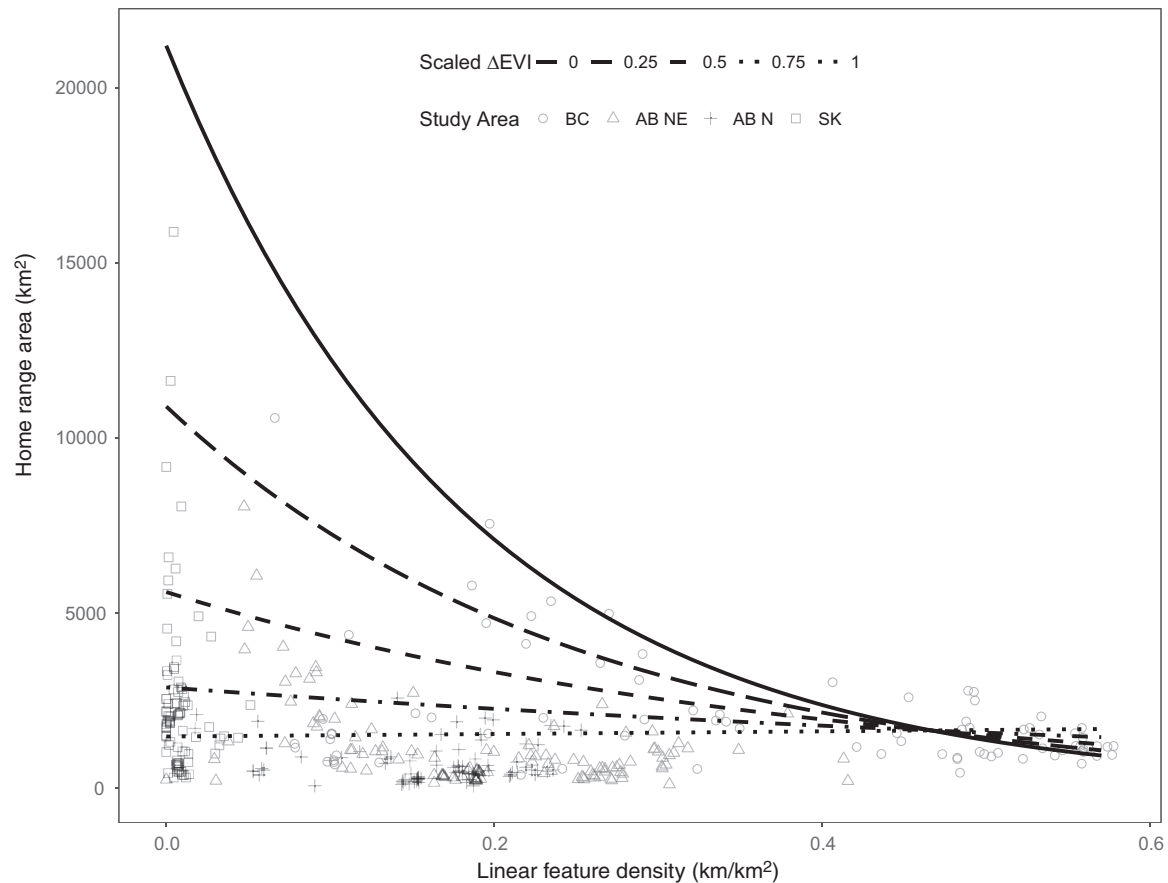


FIGURE 4 Wolf seasonal home range area (km^2), calculated using individual 95% autocorrelated density estimators, as a function of linear feature density (km/km^2) and primary productivity (ΔEVI [Enhanced Vegetation Index], scaled between 0 and 1) within each home range. Raw values are presented as points for each study subregion, and the predicted relationship is shown for the reference categories (snow season and BC) with monitoring period set to the mean. AB NE, northeastern Alberta; AB N, northern Alberta; BC, British Columbia; SK, Saskatchewan

were 1.12 ($\text{SE} = 0.07$) times larger than predicted home ranges.

DISCUSSION

We assessed whether resource density, resource exploitation, or the interaction between the two influenced the home range size of wolves, which are an apex predator in North America's boreal forests. We found that wolf home range size was influenced by the interaction between linear feature density and primary productivity, suggesting that linear features increase the "effective" density of resources by increasing the energy gained per unit time and distance, while reducing energy spent (Charnov, 1976; Pyke et al., 1977). We then evaluated the support for two competing hypotheses linking exploitation efficiency to home range size. Wolf home range size decreased as linear feature density increased, supporting the Exploitation Efficiency Hypothesis. The effect of linear features on home range size diminished in more productive areas, suggesting that exploitation

efficiency is of greater importance when resource density is low. Our results suggest that facilitated access to prey can increase regional consumer density, which is supported by studies that found that wolf habitat use and density increased with disturbance-mediated productivity (Kittle et al., 2017; Serrouya et al., 2021).

Increased movement is typically predicted to increase encounter rates between consumers and resources, therefore increasing kill rates (Holling, 1959a; Morales et al., 2010). Under the Diffusion Hypothesis, movement costs could even become so low that predators only consume the highest quality portion of the food item before moving to the next prey item, resulting in surplus killing (DelGuidice, 1998). However, under the Exploitation Efficiency Hypothesis kill rates may instead remain constant, or even decrease, if facilitated movement decreases the energy required to survive and reproduce, as suggested by our results. Although kill rates within each home range may not increase as energy requirements decrease, higher predation rates may still occur at a regional scale because small wolf home ranges may result

in higher wolf densities as more home ranges can be “packed” into the landscape (Wang & Grimm, 2007). More efficient predators may even be able to devote more energy to reproduction, leading to a feedback between the functional and numerical response (Holling, 1959b).

In the case of prey populations limited by predation, an increased predation rate will decrease the density of prey (Holling, 1959a), having top-down consequences on the food chain. Increasing the exploitative efficiency of predators should decrease the prey density needed for a given predator density to be sustained (Rosenzweig & MacArthur, 1963), resulting in a system that moves away from a stable equilibrium, therefore becoming cyclic and more sensitive to stochastic events. Understanding how facilitated exploitation of a given resource density effects kill rates, predation rates, and predator–prey interactions is fundamental to predicting responses to landscape change.

Wolves are territorial (Mech & Boitani, 2003) and, as such, intraspecific aggression associated with territorial defense decreases survival and is hypothesized to limit wolf populations (Cubaynes et al., 2014). Increased movement efficiency may also facilitate territory-defense behaviors such as patrolling and scent marking. Reducing the cost of these behaviors may allow some species to defend larger territories, thereby increasing access to resources (Moorcroft & Lewis, 2006). Sells et al. (2021) also observed smaller wolf territories in areas with higher road density, and posited that this effect was due to decreased cost of travel despite pointing out the perplexity that territory size should increase as a result of decreased defensive costs. Because smaller home ranges have a higher perimeter to volume ratio, the relative cost of territorial defense may in fact be higher with smaller home ranges. Our finding that increased linear feature density was related to smaller home ranges suggests that exploitation efficiency overcomes the added cost of higher defense costs. With the increased availability of movement datasets across taxa, future work should test the role of resource density and exploitation efficiency across territorial and non-territorial species to understand the relative role of territory defense.

While we found that increased linear feature density decreased wolf home range size in our system, there may be nonlinear effects that were not observed in our study. There is likely a point in which further increases in linear features no longer facilitate movement or even disrupt movement (Muhly et al., 2019). In this situation, diffusion facilitation may play a more prominent role and home range size may increase with increasing linear feature density. Further, increased linear feature density may even pose costs to wolves and their prey. For example, linear features may facilitate human access, thereby increasing hunter harvest of ungulates (Rempel

et al., 1997). In this case, increased linear feature density likely does not represent increased exploitation efficiency, but instead depressed prey density. In systems where roads that are used frequently by humans are the predominant linear feature, movement may not be facilitated and instead lead to increased home range size (Thompson et al., 2021). Because boreal western Canada has relatively low human population densities, human use of linear features is low (Appendix S1); particularly for seismic lines and pipelines (Pigeon et al., 2016). We posit that we did not observe nonlinear patterns in our study system because the predominant linear features increase wolf hunting efficiency but confer relatively low costs to wolves and their prey.

Our finding that home ranges are smaller in areas with increased resource density is predicated on the assumption that primary productivity is a measure of wolf prey density (Serrouya et al., 2021; Street et al., 2015). We found that moose density, a primary prey species for wolves in these systems (Fuller & Keith, 1980; James et al., 2004), increased with increasing primary productivity, supporting this assumption. However, invading white-tailed deer (*Odocoileus virginianus*) populations are increasingly becoming a dominant prey species for wolves (Latham et al., 2011, 2013). While primary productivity is a reasonable index of ungulate density in the boreal forest, other prey species such as beavers (Latham et al., 2013) are not accounted for in our analyses. Diet composition likely influences the caloric gains relative to the caloric costs associated with foraging and consumption, as well as the distribution and abundance of resource patches (Ford, 1983; MacArthur & Pianka, 1966). We expect that movement between resource patches, that is, resource exploitation, becomes increasingly important for smaller prey with lower handling time. However, the relationship between consumer density, home range size, and the density of various prey species should be further explored.

The link between resource density, resource exploitation, and home range size has applied implications for species management. In the system we present here, restoration of linear features is identified as a priority for the management and recovery of threatened woodland caribou (Environment Canada, 2014). The interaction between linear feature density and primary productivity suggests that restoring linear features in areas of low productivity will have disproportionately large effects by simultaneously decreasing foraging efficiency and regional wolf density. In contrast, in high-productivity areas, decreasing vagility may reduce foraging efficiency (Johnson et al., 2019; Serrouya et al., 2020; Spangenberg et al., 2019), but will not effect home range size and thus regional density. Our work adds to the growing demand for studies to better link movement ecology and ecological theory to conservation (Allen & Singh, 2016).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Dickie et al., 2021) are available in Dryad at <https://doi.org/10.5061/dryad.ns1rn8pth>. Code and associated data (Melanie Dickie, 2021) are available in Zenodo at <https://doi.org/10.5281/zenodo.5643218>.

ORCID

Melanie Dickie  <https://orcid.org/0000-0003-2177-2352>
 Robert Serrouya  <https://orcid.org/0000-0001-5233-6081>
 Tal Avgar  <https://orcid.org/0000-0002-8764-6976>
 Craig DeMars  <https://orcid.org/0000-0001-7984-633X>
 Stan Boutin  <https://orcid.org/0000-0001-6317-038X>
 Adam T. Ford  <https://orcid.org/0000-0003-2509-7980>

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