

# Living on the edge: spatial response of coyotes (*Canis latrans*) to wolves (*Canis lupus*) in the subarctic

Kaija Klaunder, Bridget L. Borg, and Laura R. Prugh

**Abstract:** Understanding how mesopredators manage the risks associated with apex predators is key to explaining impacts of apex predators on mesopredator populations and patterns of mesopredator space use. Here we examine the spatial response of coyotes (*Canis latrans* Say, 1823) to risk posed by wolves (*Canis lupus* Linnaeus, 1758) using data from sympatric individuals fitted with GPS collars in subarctic Alaska, USA, near the northern range limit for coyotes. We show that coyotes do not universally avoid wolves, but instead demonstrate season-specific responses to both wolf proximity and long-term use of the landscape by wolves. Specifically, coyotes switched from avoiding wolves in summer to preferring areas with wolves in winter, and this selection was consistent across short-term and longer term temporal scales. In the summer, coyotes responded less strongly to risk of wolves when in open areas than when in closed vegetation. We also demonstrate that coyotes maintain extremely large territories averaging 291 km<sup>2</sup>, and experience low annual survival (0.50) with large carnivores being the largest source of mortality. This combination of attraction and avoidance predicated on season and landcover suggests that mesopredators use complex behavioral strategies to mediate the effects of apex predators.

**Key words:** coyote, *Canis latrans*, wolf, *Canis lupus*, habitat selection, risk, subarctic.

**Résumé :** La compréhension de la gestion que font les mésoprédateurs des risques associés aux superprédateurs est d'importance clé pour expliquer les impacts de superprédateurs sur les populations de mésoprédateurs et les motifs d'utilisation de l'espace de ces derniers. Nous examinons la réaction spatiale de coyotes (*Canis latrans* Say, 1823) au risque posé par les loups (*Canis lupus* Linnaeus, 1758) en utilisant des données sur des individus sympatriques munis de colliers GPS en Alaska (États-Unis) subarctique, près de la limite septentrionale de l'aire de répartition des coyotes. Nous démontrons que les coyotes n'évitent pas universellement les loups, mais présentent plutôt différentes réactions selon la saison tant à la proximité des loups qu'à l'utilisation à long terme du paysage par ces derniers. Plus précisément, les coyotes passent de l'évitement des loups en été à une préférence pour des secteurs renfermant des loups en hiver, et cette sélection est cohérente à des échelles temporelles aussi bien courtes que longues. En été, les coyotes réagissent moins fortement au risque posé par les loups quand ils sont dans des secteurs ouverts que dans des secteurs à végétation fermée. Nous démontrons également que les coyotes maintiennent des territoires extrêmement vastes, faisant en moyenne 291 km<sup>2</sup>, et qu'ils présentent un faible taux de survie annuelle (0,50), les grands carnivores constituant la plus grande cause de mortalité. Cette combinaison d'attraction et d'évitement en fonction de la saison et de la couverture du sol indiquerait que les mésoprédateurs emploient des stratégies comportementales complexes pour moduler les effets des superprédateurs. [Traduit par la Rédaction]

**Mots-clés :** coyote, *Canis latrans*, loup, *Canis lupus*, sélection de l'habitat, risque, subarctique.

## Introduction

The risk of injury or death by predation is a key driver of animal behavior (Thomson et al. 2006; Valeix et al. 2009; Laundré et al. 2010; Oriol-Cotterill et al. 2015; Breed et al. 2017). Because risk varies in time and space, at-risk individuals can use behavioral strategies to take advantage of spatial and temporal windows of reduced risk (Lima and Bednekoff 1999; Valeix et al. 2009; Bischof et al. 2014; Stewart et al. 2016). Response strategies to risk can be broadly classified as reactive or predictive (Valeix et al. 2009; Broekhuis et al. 2013; López-Bao et al. 2016). A reactive response to risk is based on the immediate proximity of a predator, while a predictive response is based on consistent patterns of predator use — for example, avoiding areas or times with frequent predator activity. A reactive risk response can therefore

be described as one which is sensitive to short-term risk, and a predictive response as one which is sensitive to long-term risk.

Response to risk of predation has primarily been studied for prey species, yet it also applies to many predator species at risk from larger competitors (Palomares and Caro 1999; Lourenço et al. 2014; Oriol-Cotterill et al. 2015). Demographically, larger carnivores have been shown to suppress mesocarnivore populations, but despite continued study of intraguild population dynamics, the patterns and mechanisms of mesocarnivore suppression and release remain inconclusive (Elmhagen and Rushton 2007; Ford and Goheen 2015; Allen et al. 2017a; Bergstr et al. 2017). It has been hypothesized that changes in habitat use driven by predation risk facilitate this suppression, analogous to the effects of the “landscape of fear” on prey species (Schmitz et al. 1997;

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Prugh et al. 2009; Ritchie and Johnson 2009; Elmhagen et al. 2010; Laundré et al. 2010; Lourenço et al. 2014).

Despite the threat of interspecific killing, mesocarnivores may also benefit from proximity to large carnivores by gaining access to carrion resources or by using large carnivore presence as a shield against competition and risk from other mesocarnivores (Switalski 2003; Khalil et al. 2014; Allen et al. 2015, 2017b; though for the potential negative consequences of scavenging see Prugh and Sivy 2020). This trade-off serves as an incentive for mesocarnivores to respond flexibly to large carnivore risk depending on the circumstances. Thus, it is not surprising that spatial behavioral responses of mesocarnivores to large carnivores have not always demonstrated patterns of avoidance as might be assumed (Ritchie and Johnson 2009; Swanson et al. 2014; Balme et al. 2017; Sivy et al. 2017b). Additional research is needed to establish when and how mesocarnivores avoid or are attracted to large carnivore activity, whether they tend to be reactive or predictive in their response to large carnivore presence, and if their response is flexible based on factors such as landcover and season.

The recent recolonization by gray wolves (*Canis lupus* Linnaeus, 1758) of many parts of their historic range in North America has led to considerable research documenting the ecological changes following recolonization, including suppressive effects on coyote (*Canis latrans* Say, 1823) populations (Berger and Gese 2007; Berger et al. 2008; Merkle et al. 2009; Latham et al. 2013; Ripple et al. 2013). It has been hypothesized that widespread extirpation of wolves (including the red wolf (*Canis rufus* Audubon and Bachman, 1851) and the eastern (or timber) wolf (*Canis lupus lycaon* Schreber, 1775), as well as *C. lupus*) facilitated the coyote's massive range expansion over the past 300 years (Thurber and Peterson 1991; Berger and Gese 2007; Berger et al. 2008; Gese et al. 2008; Ripple et al. 2013). However, coyotes were historically sympatric with gray wolves, and expanded their range into Canada and Alaska (USA), regions with robust gray wolf populations, as well as eastward into the remnant ranges of eastern and red wolves, suggesting that coyotes maintain successful strategies for sharing landscapes with wolves (Hody and Kays 2018). Given the abundant examples of gray wolves (hereafter "wolves") killing coyotes, wolves clearly represent a threat; conversely, coyotes successfully co-occur with wolves in many areas and have been documented scavenging from wolf kills, sometimes extensively (Thurber 1992; Palomares and Caro 1999; Switalski 2003; Berger and Gese 2007; Merkle et al. 2009). There is conflicting evidence on the key question of whether coyotes avoid wolves, ignore wolves, or are attracted to wolves at local spatial scales (Berger and Gese 2007). In the cases demonstrating avoidance of wolves by coyotes, there is evidence for both reactive (e.g., Atwood and Gese 2010) and predictive (e.g., Arjo and Pletscher 1999; Benson and Patterson 2013) avoidance. Only two previous studies have used GPS-collar technology on sympatric gray wolves and coyotes (Benson and Patterson 2013; Latham et al. 2013), and of these, only Benson and Patterson (2013) directly evaluated coyote-wolf interactions. Thus, fine-scale spatial information needed for detailed examination of coyote-wolf interactions has been lacking.

In areas of northern coyote range expansion, limited information is available about the ecology of coyotes and their relationship to wolves (Thurber 1992; Latham et al. 2013; Sivy et al. 2017b). Populations at the edge of a species' range may exhibit altered behavior, ecology, or genetics compared with central populations, and offer unique insight into evolutionary processes (Sexton et al. 2009). Prior research on coyotes at high latitudes has documented a strong relationship between coyote and cyclic snowshoe hare (*Lepus americanus* Erxleben, 1777) populations, as well as strong reliance on carrion as an alternative food source (Theberge and Wedeles 1989; Prugh 2005; Prugh et al. 2008). Coyotes are also documented to impact mountain sheep populations through neonate consumption, with the impact mediated by snowshoe

hare abundance and wolf-induced mortality rates (Arthur 2003; Arthur and Prugh 2010). Together, these studies suggest that coyotes have the potential to play important roles in community structure, and that their relationship with wolves may mediate their community-wide impacts.

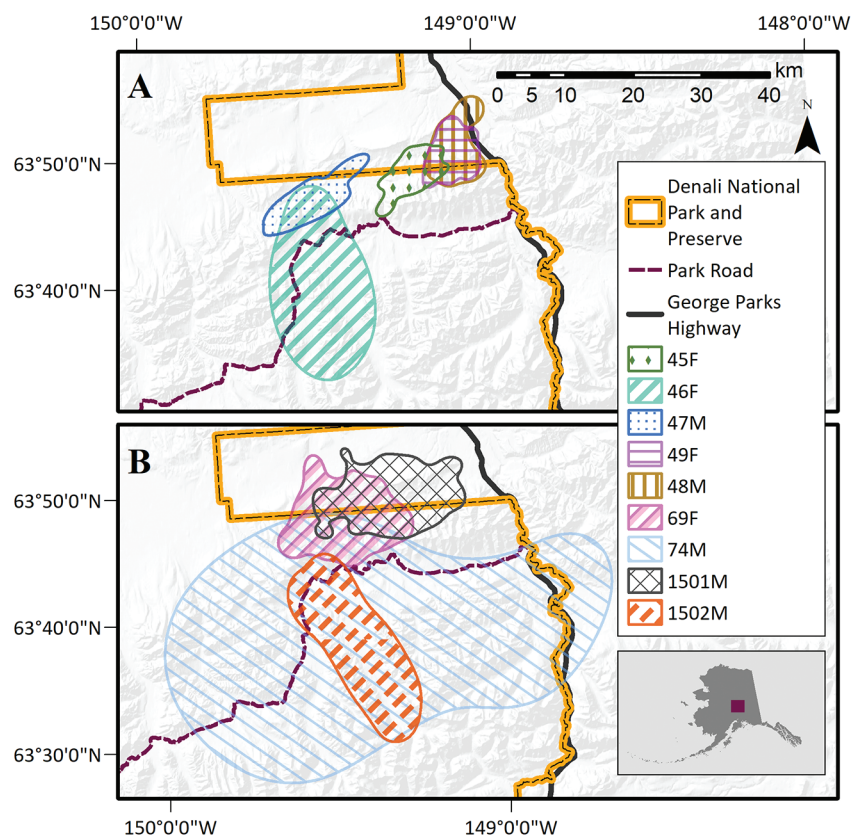
In this paper, we examine coyote response to wolf risk in a subarctic environment using data from sympatric GPS-collared wolves and coyotes in Denali National Park and Preserve (DNPP), Alaska, a subarctic environment with a full suite of endemic carnivores that was colonized by coyotes beginning circa 1920 (Karstens 1928; Hody and Kays 2018). Specifically, we examine whether coyotes respond reactively or predictively to wolves by quantifying coyote spatial responses to wolf proximity and long-term wolf use, respectively. We also determine whether these responses are influenced by season and landscape features, and estimated survival of collared coyotes to determine the extent of mortality risk represented by wolves. We predicted that coyotes would reactively avoid wolves but not respond to long-term wolf use, allowing them to optimize habitat selection and potentially take advantage of carrion in a harsh environment with limited prey base. We predicted that avoidance would be strongest in areas of thick vegetation with poor visibility, and in the summer when small prey are more readily available. We predicted that if coyotes did show attraction to wolves at either temporal scale, then it would be during the winter, when the potential rewards offered by carrion may be the most important.

## Materials and methods

### Study area

This study took place in the north-eastern portion of Denali National Park and Preserve and adjacent state and private lands (Fig. 1). The area is characterized by a subarctic climate with lengthy cold winters and cool summers. Mean annual precipitation is 38 cm, with mean winter and summer temperatures of  $-15$  and  $12$  °C, respectively (Sousanes 2016). Elevation ranged from 373 to 2080 m. Low elevations are characterized by mixed spruce (genus *Picea* A. Dietr.) and deciduous forest (black cottonwood (*Populus trichocarpa* Torr. and A. Gray ex Hook.), birch (genus *Betula* L.), and aspen (*Populus tremuloides* Michx.)), with willow (genus *Salix* L.) and alder (genus *Alnus* Mill.) along riparian corridors and braided glacial rivers. Taiga and shrub (willow and dwarf birch (*Betula nana* L.)) make up the bulk of the middle elevations, rising to alpine vegetation on the higher slopes. Available small prey species include snowshoe hare, microtine rodents, Arctic ground squirrel (*Urocitellus parryii* (Richardson, 1825)), hoary marmots (*Marmota caligata* (Eschscholtz, 1829)), ptarmigan (genus *Lagopus* Brisson, 1760), and grouse (Ruffed Grouse, *Bonasa umbellus* (Linnaeus, 1766); Spruce Grouse, *Falciptennis canadensis* (Linnaeus, 1758)). Ungulates include moose (*Alces alces* (Linnaeus, 1758)), caribou (*Rangifer tarandus* (Linnaeus, 1758)), and Dall's sheep (*Ovis dalli* Nelson, 1884). Other carnivore species present include wolves, grizzly and black bears (*Ursus arctos* Linnaeus, 1758 and *Ursus americanus* Pallas, 1780, respectively), wolverines (*Gulo gulo* (Linnaeus, 1758)), red fox (*Vulpes vulpes* (Linnaeus, 1758)), lynx (*Lynx canadensis* Kerr, 1792), and marten (*Martes americana* (Turton, 1806)). Trapping and hunting of coyotes and wolves is legal on state lands. Trappers and hunters are not required to report annual coyote take, but voluntary reporting to Alaska Department of Fish and Game suggests very low annual take (averaging 0–2 individuals) from the subunit containing this study area (Parr 2016, 2017). Annual trapping of wolves has been found not to reduce the regional population, and it does not prevent wolf residency on state lands (Borg et al. 2015). There is limited human presence throughout most of the study area, and it is concentrated around roads and the few established trails.

**Fig. 1.** Map of coyote (*Canis latrans*) home ranges in Denali National Park and Preserve, Alaska, USA. Coyote 95% autocorrelated kernel density home ranges for individuals captured in (A) 2013 and (B) 2014–2015, displayed separately for visual clarity, are depicted with polygons. Inset shows the location of the study area within Alaska. Letters M and F following coyote ID denotes male and female, respectively. Figure was created using ArcMap version 10.7.1 (Esri, Inc. 2019) and assembled from the following data sources — topography layer: National Elevation Dataset (United States Geological Survey 2002); roads: National Park Service (NPS 2014); park outline: NPS; state of Alaska coastline: Alaska Department of Natural Resources (2008). Color version online.



### Fieldwork

Coyotes were collared during March 2013–2015. Coyotes were darted from a helicopter, immobilized with a combination of tiletamine hydrochloride and zolazepam hydrochloride, and examined for age, sex, and health. Age was determined by tooth wear. Coyotes were fitted with Telonics GPS store-on-board collars (model TTW-4400; Telonics, Inc., Mesa, Arizona, USA) with a 2-year deployment period and automatic drop-off. In 2013, collars were programmed to record locations every 24 h; in subsequent years the fix interval was altered to every 3 h. Coyote collars were retrieved after the death of the animal or after programmed drop-off, whichever came first. Mortality sites were investigated and necropsies performed to determine cause of death when possible. As part of the long-term wolf monitoring program, DNPP staff deployed and maintained 1–3 GPS collars on wolves in each wolf pack that occurred in the study area, generally on breeding animals. Wolves were darted from helicopters, immobilized with a combination of tiletamine hydrochloride and zolazepam hydrochloride, and fitted with Telonics GPS collars (multiple models; Telonics, Inc., Mesa, Arizona, USA; for protocol details see Meier et al. 2009). Wolf collar fix intervals varied between 4 and 24 h. Capture and handling procedures for wolves and coyotes were approved under National Park Service (NPS) Institutional Animal Care and Use Committee protocols AKR\_YUCH and DENA\_Burch\_Wolves\_2013.

### Coyote home range and survival

Coyote home ranges were calculated using autocorrelated kernel density estimation (Fleming et al. 2015; Fleming and Calabrese

2017), available in the R package “ctmm” (Calabrese et al. 2016). This technique refines classic kernel density estimation by explicitly modeling the degree of autocorrelation of locations for each individual before calculating the home range, thus replacing the correlated random walk model framework, which assumes independent locations, with the more appropriate continuous-time stochastic process framework (Fleming and Calabrese 2017). Location data for each coyote were screened for inaccurate locations and extra-territorial forays, and variograms were visually examined to ensure model assumptions of territoriality were met. The autocorrelation of the locations was then fit to five possible movement models, including a null model of complete independence, and the top model was selected with Akaike’s information criterion (AIC) (Calabrese et al. 2016). The top model was then used in combination with the location data to estimate an appropriate smoothing bandwidth, and the 95% home-range kernel density estimate was generated using the function “akde” (Calabrese et al. 2016). This process was repeated for each coyote, and the resulting 95% home-range isopleths delineated the “available” area for each coyote used in the resource selection function. We calculated annual coyote survival rates, mortality due to harvest, and mortality due to wolves using a staggered-entry Kaplan–Meier model (Pollock et al. 1989) with monthly time intervals.

### Analysis

Because we expect that coyote space use is influenced by a variety of landscape features as well as response to wolves, we used a resource selection function (RSF) framework to examine coyote



responses to wolf risk while also accounting for landscape features. We chose a RSF framework over a movement-based step-selection function framework because the long intervals between locations in some cases (4–24 h fix intervals) made a movement-based approach less appropriate, especially for evaluating response to wolf proximity (Avgar et al. 2016). Because of the extreme seasonal changes in the subarctic, we modeled summer and winter seasons separately.

### Wolf risk variables

We used two wolf risk variables in the analyses. The first, distance to the nearest wolf, represented short-term risk. The second, long-term wolf use intensity, represented long-term risk. To calculate distance to wolf, we identified all wolf locations within  $\pm 12$  h of each coyote location (used and available), calculated the distance to each in metres, and selected the minimum. Twelve hours was chosen because it allowed for the inclusion of all wolf collar daily location times, ensuring that calculations were not biased towards wolves with shorter fix intervals. To create a quantitative measure of long-term wolf use intensity, we created localized density distributions (LDDs) for winter and summer. LDDs are a measure of use similar to traditional utilization distributions (UDs), but weighted by the number of individuals in a social group (Kittle et al. 2015, 2017). This approach accounted for the likely greater threat that larger wolf packs represent compared with pairs or smaller packs of wolves. To do this, we first used “ctmm” to generate UD rasters for each collared wolf by season and year, as described above for coyotes. We included individuals in a given season only if they had been monitored for at least 3 months of the 6-month season and did not disperse during that time. If there was more than one collared individual in a pack, we merged the individual UD, averaging overlapping cell values. We eliminated raster values  $< 0.05$  to create a 95% isopleth raster for that pack-season and integrated pack UD values to one to standardize values across packs with different size territories. We then multiplied the cell values of each UD by the number of individuals in the pack, as determined by the official DNPP counts at the beginning of that season, which are based on multiple aerial sightings and track counts and photographs. This created an LDD. We then combined the LDDs of each pack within each season, summing overlapping values, and integrated the resulting LDD to one. Finally, we combined the seasonal LDDs across years, averaging overlapping cells, to produce rasters that represented mean summer and winter use by wolves, weighted by pack size (Supplementary Fig. S1).<sup>1</sup> These rasters were then integrated to one to allow model coefficients to be directly compared.

### Landscape variables

We selected five landscape variables to be tested in the RSF: elevation, slope, aspect, distance to linear feature, and vegetation type. Elevation, slope, and aspect were generated from a 5 m digital terrain model (United States Geological Survey 2010). Aspect was binned into north, east, south, or west. Linear features comprised waterways and trails. We obtained a map of waterways from the National Hydrography Dataset (United States Geological Survey 2013), and we removed waterway segments above 1100 m in elevation. This was necessary to eliminate waterways that could not function as viable travel ways; in this study system, such high-elevation waterways are brush-choked ravines. Summer and winter trails were available in DNPP GIS databases. We defined “summer” as being April through September and “winter” as being October through March, which generally corresponded to snow-free and snow-covered periods, respectively. The vegetative cover layer was drawn from the 2011 National Landcover Database (Homer et al. 2015). Based on description and distribution,

**Table 1.** Mean annual survival of collared coyotes (*Canis latrans*) in Denali National Park and Preserve, Alaska, USA.

Year	At risk	Died	Survival	SD
2013	5	2	0.60	0.17
2014	5	3	0.40	0.14
2015	3	2	0.33	0.16
2016	1	0	1	—
Total	14	7	—	—
Mean	—	—	0.5	0.16

we binned the landcover classes into three categories: “open”, which included alpine vegetation, dwarf shrub, and bare ground; “closed”, which included evergreen and mixed deciduous forests; “shrub”, which included shrub-scrub and taiga areas. These three categories represent differing degrees of visual range, as well as capturing the three basic landscape cover types.

### Available locations

When generating “available” locations in a used-available design, it is critical to ensure that available locations adequately sample the landscape variables (Northrup et al. 2013). To this end, we generated a grid of points with 100 m spacing across the merged 95% coyote home ranges and extracted the landscape variable values at each point. We then subsampled this “census” at resolutions of 200 m, 400 m, 1 km, 2 km, 4 km, and 8 km, examining mean and coefficient of variation (CV) of each variable for evidence of destabilization. We found that mean and CV remained stable for all variables up to the 400 m resolution, but to be conservative, we used a 200 m grid (one point per 0.02 ha) as the target sampling density. To achieve this for both summer and winter models, we generated points at a density of one per 0.01 ha in each coyote territory, and then assigned each point a random date and time drawn from the window of the collar deployment of that coyote, thus subdividing the points into summer and winter, with each having an approximate density of one per 0.02 ha. At each available point, we extracted variable values, including long-term wolf risk, and calculated distance to nearest wolf within a  $\pm 12$  h window.

### Resource selection modeling

We examined all covariates for collinearity using a correlation matrix of the values of the 100 m census grid, specifically looking for cases where Spearman’s correlation values were greater than 0.6. We found that elevation was highly correlated with slope ( $r = 0.64$ ) and distance to linear features ( $r = 0.67$  for summer and  $r = 0.68$  for winter), and since the latter are more biologically informative, we discarded elevation.

Because coyote responses to distance from wolves and landscape features could be nonlinear, we investigated logarithmic and polynomial response forms. We found that coyote responses to slope and distance to linear feature were best represented by a quadratic function, and that response to distance from wolf was linear and required no transformation.

To model coyote habitat selection and response to wolf risk, we used generalized linear mixed models with binomial response and logit link. Because individuals in the same social group are likely to have similar movements, we included individual coyote ID nested within pair ID as a random intercept for both summer and winter. We scaled all continuous predictors to mean of zero and standard deviation (SD) of one to improve model convergence. Per our hypotheses, we included interactions between vegetation and both forms of wolf risk to see if risk response was

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2020-0050>.

**Table 2.** Top five resource selection function models (out of 416), based on Akaike's information criterion (AIC) ranking, for coyotes (*Canis latrans*) in winter (October–March) and summer (April–September) in Denali National Park and Preserve, Alaska, USA.

Model	K	Log-likelihood	AIC	$\Delta$ AIC	Akaike weight
<b>Winter</b>					
slope + slope <sup>2</sup> + aspect + distance to wolf + vegetation type × long-term wolf use + distance to linear feature + distance to linear feature <sup>2</sup> + 1   CoyoteID	15	−18 660.01	37 350.02	0	0.8333
slope + slope <sup>2</sup> + aspect + vegetation type × distance to wolf + vegetation type × long-term wolf use + distance to linear feature + distance to linear feature <sup>2</sup> + 1   CoyoteID <sup>a</sup>	17	−18 659.68	37 353.37	3.354681	0.1557
slope + slope <sup>2</sup> + aspect + distance to wolf + vegetation type × long-term wolf use + distance to linear feature + 1   CoyoteID	14	−18 666.1	37 360.2	10.181981	0.0051
slope + slope <sup>2</sup> + aspect + vegetation type × long-term wolf use + distance to linear feature + distance to linear feature <sup>2</sup> + 1   CoyoteID	14	−18 666.16	37 360.32	10.306443	0.0048
slope + slope <sup>2</sup> + aspect + vegetation type × distance to wolf + vegetation type × long-term wolf use + distance to linear feature + 1   CoyoteID	16	−18 665.77	37 363.54	13.520857	0.0010
<b>Summer</b>					
slope + slope <sup>2</sup> + aspect + distance to wolf + vegetation type × long-term wolf use + distance to linear feature <sup>2</sup> + 1   CoyoteID	14	−27 670.65	55 369.3	0.000	0.5894
slope + slope <sup>2</sup> + aspect + distance to wolf + vegetation type × long-term wolf use + distance to linear feature + distance to linear feature <sup>2</sup> + 1   CoyoteID	15	−27 670.48	55 370.95	1.656	0.2576
slope + slope <sup>2</sup> + aspect + vegetation type × distance to wolf + vegetation type × long-term wolf use + distance to linear feature <sup>2</sup> + 1   CoyoteID	16	−27 670.36	55 372.72	3.420132	0.1066
slope + slope <sup>2</sup> + aspect + vegetation type × distance to wolf + vegetation type × long-term wolf use + distance to linear feature + distance to linear feature <sup>2</sup> + 1   CoyoteID <sup>a</sup>	17	−27 670.19	55 374.39	5.090112	0.0462
slope + slope <sup>2</sup> + aspect + distance to wolf + vegetation type × long-term wolf use + distance to linear feature + 1   CoyoteID	14	−27 679.12	55 386.24	16.945121	0.0001

Note: K is the number of parameters.

<sup>a</sup>Full model.

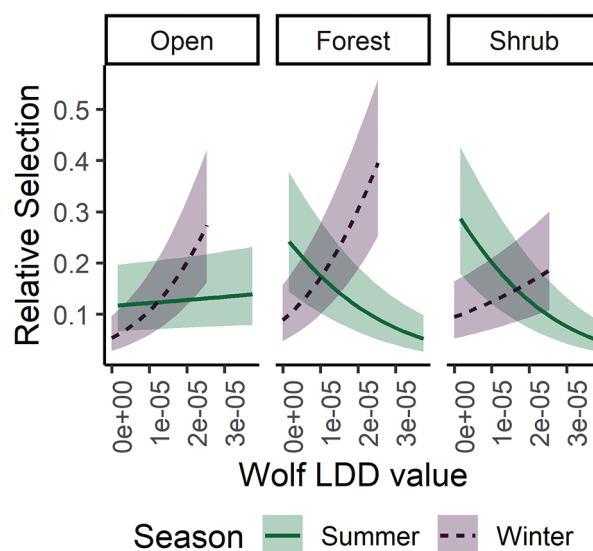
feature-specific. We thus began with a global model of the form “use = slope + slope<sup>2</sup> + distance to linear feature + distance to linear feature<sup>2</sup> + aspect + vegetation × distance to wolf + vegetation × long-term wolf use + (1 | PairID/CoyoteID)” for summer and winter, respectively. We used the “dredge” function from package “MuMin” (Barton 2018) to run all possible subsets of the global model and rank them by AIC (Burnham and Anderson 2002). The top model was validated using five-fold random cross-validation, and four-fold cross-validation with individual blocking, with two coyotes per fold (Boyce et al. 2002; Roberts et al. 2017). Because observed values of distance to wolf ranged as high as 150 km, we ran a secondary analysis where we included the same landscape and wolf risk variables but restricted locations to those less than 5 km from the nearest wolf, presenting a biologically appropriate framework for evaluating response to wolf proximity. Five kilometres was identified as best fulfilling a trade-off between detection ability, which diminishes with increasing distance, and analytical power, which increases as more points are included. Thus, we constructed a total of four models: primary summer and winter models including all points, and secondary summer and winter models with restricted locations, for the purpose of assessing response to wolf proximity.

## Results

### Coyote survival and home-range size

Nine adult coyotes were collared, five males and four females, ranging in age from 2 to 4 years old (Supplementary Table S1 and Fig. S2).<sup>1</sup> Males weighed a mean of 13.9 kg (SE = 0.1 kg) and females weighed a mean of 12.8 kg (SE = 0.6 kg). One female (46F) was recollared after 1 year and switched from a 24 h to a 3 h fix interval. One male (47M) was legally trapped only 56 days after collaring and was therefore excluded from the RSF. All coyotes were determined to be resident based on a combination of age, presence of mate at time of capture ( $n = 8$  had a mate present), and subsequent locations. In three instances, both members of the pair were collared: 46F and

**Fig. 2.** Effect of vegetation type (open, closed, shrub), season (summer, green solid line; winter, purple broken line), and long-term wolf (*Canis lupus*) use (localized density distribution (LDD) value; see Materials and methods) on relative habitat selection by coyotes (*Canis latrans*) in Denali National Park, Alaska, USA. Error bars show 95% confidence intervals as determined from fixed effects only. Color version online.



47M, 48M and 49F, and 46F and 74M (after the death of previous mate 47M). Mean duration of deployment was 465 days (SE = 78.5 days). In total, the collars generated 18 808 territorial locations and allowed a survival analysis on 14 animal-years of data. Mean annual survival of coyotes was 0.5 (SD = 0.09; Table 1). Mean annual mortality from

**Table 3.** Effects of environmental variables and wolf (*Canis lupus*) risk variables on coyote (*Canis latrans*) habitat selection in Denali National Park, Alaska, USA.

Fixed effects	Summer			Winter		
	Odds ratio	95% CI	<i>p</i>	Odds ratio	95% CI	<i>p</i>
(Intercept)	0.12	0.06–0.25	<0.001	0.08	0.05–0.20	<0.001
Slope	4.78	4.34–5.27	<0.001	2.96	2.65–3.30	<0.001
Slope squared	0.17	0.15–0.19	<0.001	0.35	0.31–0.39	<0.001
Aspect						
Aspect: East	1.10	1.03–1.17	0.003	1.18	1.09–1.27	<0.001
Aspect: South	1.35	1.27–1.44	<0.001	1.87	1.73–2.02	<0.001
Aspect: West	1.32	1.25–1.40	<0.001	1.29	1.20–1.39	<0.001
Distance to linear feature (summer)	1.02	0.95–1.10	0.558			
Distance to linear feature squared (summer)	0.84	0.77–0.91	<0.001			
Vegetation						
Vegetation: Closed	1.17	1.07–1.27	<0.001	1.73	1.57–1.92	<0.001
Vegetation: Shrub	1.34	1.26–1.43	<0.001	1.20	1.10–1.30	<0.001
Distance to nearest wolf	0.93	0.91–0.95	<0.001	0.95	0.93–0.98	<0.001
Summer long-term wolf use intensity	1.04	0.99–1.09	0.138			
Veg:Closed × Summer long-term wolf use intensity	0.70	0.63–0.77	<0.001			
Veg:Shrub × Summer long-term wolf use intensity	0.67	0.63–0.71	<0.001			
Distance to linear feature (winter)				0.60	0.55–0.66	<0.001
Distance to linear feature squared (winter)				1.25	1.10–1.40	<0.001
Winter long-term wolf use intensity				1.45	1.34–1.57	<0.001
Veg:Closed × Winter long-term wolf use intensity				1.00	0.89–1.12	0.986
Veg:Shrub × Winter long-term wolf use intensity				0.80	0.73–0.88	<0.001
Random effects	Summer			Winter		
Between-group variance, CoyoteID:Pair	0.38			0.17		
Between-group variance, Pair	0.20			0.45		
<i>N</i> of CoyoteID	8			8		
<i>N</i> of Pair	6			6		
Intraclass correlation coefficient (ICC)	0.15			0.16		
Observations	86 283			60 316		
Marginal <i>R</i> <sup>2</sup>	0.106			0.105		
Conditional <i>R</i> <sup>2</sup>	0.239			0.246		
Akaike's information criterion (AIC)	55 372.8			37 350.7		
Deviance	55 340.8			37 318.7		

**Note:** The 95% percentile confidence intervals (95% CI) are shown. Distances are in kilometres. Slope and distance values have been scaled and centered, scaled units are as follows. Summer: slope 11.6°; distance to linear feature 0.8 km; distance to nearest wolf 8.5 km. Winter: slope 11.5°; distance to linear feature 0.8 km; distance to nearest wolf 8.3 km. Reference level for aspect is “north” and for vegetation is “open”.

harvest was the same as that from wolves, 0.14 (SD = 0.04; Table 1), but annual mortality from all large carnivores was 0.21 (SD = 0.5; Table 1). Sources of mortality included trapping, wolves, bears, and starvation (Supplementary Table S1 and Fig. S2).<sup>1</sup> Three necropsied coyotes had multiple porcupine (*Erethizon dorsatum* (Linnaeus, 1758)) quills in their bodies at time of death.

The mean coyote home-range size was 291 km<sup>2</sup> (SE = 130 km<sup>2</sup>; Fig. 1 and Supplementary Table S2<sup>1</sup>). One coyote (74M) exhibited exceptionally wide-ranging behavior, using a home range of 1363 km<sup>2</sup>. Mean home-range size excluding this individual was 158 km<sup>2</sup> (SE = 34 km<sup>2</sup>). All coyote home ranges were encompassed by monitored wolf home ranges, with extensive overlap with four wolf packs and minor edge overlap with several additional packs. The size of overlapping wolf packs ranged from 2 to 20 individuals throughout the study period, with a mean pack size of 6 individuals.

### Model selection and validation

For primary winter model sets, AIC ranking supported the inclusion of all variables with the exception of “vegetation type × distance to wolf” (Table 2). For primary summer model sets, the top model again excluded “vegetation type × distance to wolf”, as well as “distance to linear feature”. The second-ranked summer model, with a difference of only 1.7 AIC units, included “distance to linear feature” (Table 2). Because linear terms are

conventionally included when quadratic terms are present in the model structure, we included “distance to linear feature” in the top model for summer. Both primary summer and winter models and the submodels performed acceptably under five-fold random cross-validation (Supplementary Figs. S3 and S4).<sup>1</sup> As expected, model validation worsened slightly when validated with blocking by individual (Roberts et al. 2017); however, it remained adequate for most bins, especially considering the small sample size for some individuals (Supplementary Figs. S3 and S4).<sup>1</sup>

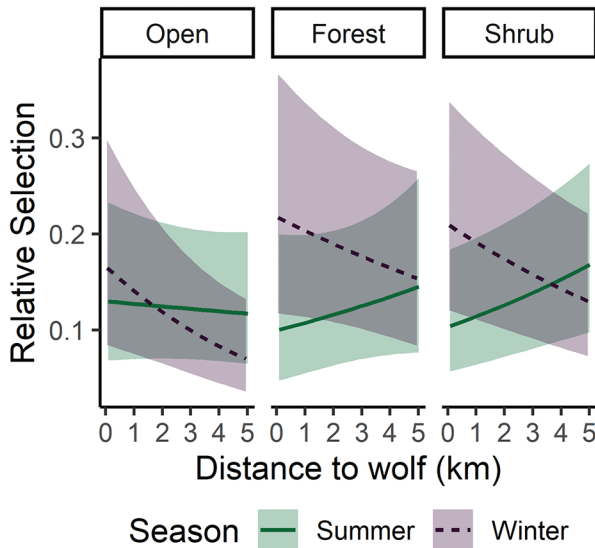
### Effects of wolf risk and landscape variables

Coyote response to long-term wolf risk varied by season and land cover (Fig. 2). In winter, coyotes selected for areas of higher long-term wolf use, especially in forested areas. In summer, coyotes selected for lower long-term wolf use in shrub and closed vegetation. Their selection in the open showed no effect of long-term wolf risk (*p* = 0.138; Fig. 2). For complete model output see Table 3.

In the secondary analysis, coyotes showed seasonal shifts in their response to wolf proximity. In summer, coyotes avoided wolf proximity in forest and shrub areas, but again showed no response in the open (*p* = 0.668; Fig. 3 and Supplementary Table S3<sup>1</sup>). In the winter, coyote locations were consistently closer to wolves than random locations across all vegetation types (Fig. 3 and Supplementary Table S3<sup>1</sup>).



**Fig. 3.** Effect of vegetation type (open, closed, shrub), season (summer, green solid line; winter, purple broken line), and distance to nearest wolf (*Canis lupus*) on relative habitat selection by coyotes (*Canis latrans*) in Denali National Park and Preserve, Alaska, USA, drawn from a subset of locations no farther than 5 km from the nearest wolf. Error bars show 95% confidence intervals as determined from fixed effects only. Color version online.



In both seasons, coyotes selected slope values of about  $20^\circ$ , slightly steeper than the most common values (Table 3). Coyotes preferred non-northern aspects in both seasons, and in winter, they specifically preferred south-facing aspects (Fig. 4 and Table 3). Coyotes selected to be nearer to linear features in both seasons, with stronger selection in winter (Fig. 4 and Table 3). Coyotes selected most strongly for shrub areas in summer and closed forest areas in winter; open areas were least selected in both seasons (Fig. 4 and Table 3).

## Discussion

We show that coyotes near the northern edge of their range in Alaska maintain very large territories and have seasonally divergent responses to wolf risk. Coyotes avoided wolves in the summer and were attracted to wolves in the winter, at both short-term and long-term time scales of selection. This pattern could suggest a potential attraction to wolf-killed carrion resources, which may be particularly important in winter due to restricted food availability and increased metabolic demands, or a shared attraction to energy-efficient travel routes. The large home-range sizes and low survival rates that we documented indicate the subarctic is a challenging place for coyotes, and their seasonal responses to wolves may help them balance the risk of interspecific killing against other key habitat needs.

Our findings indicate that coyotes employ both reactive and predictive risk mediation strategies as evidenced by their spatial response to both short-term and long-term wolf risk. Our results show that coyotes do not universally avoid wolf risk, but instead avoid wolves under some circumstances and are attracted to them (or at least do not avoid them) under others. This contrasting pattern of attraction and avoidance is in accordance with previous work in this system that used snow tracking to reveal a positive spatial relationship between wolves and coyotes at fine spatial scales and a negative relationship at landscape scales (Sivy et al. 2017b). Our findings suggest that memory, as well as sensory perception, is an important component of coyote responses to wolves. Consistent with our finding that coyotes

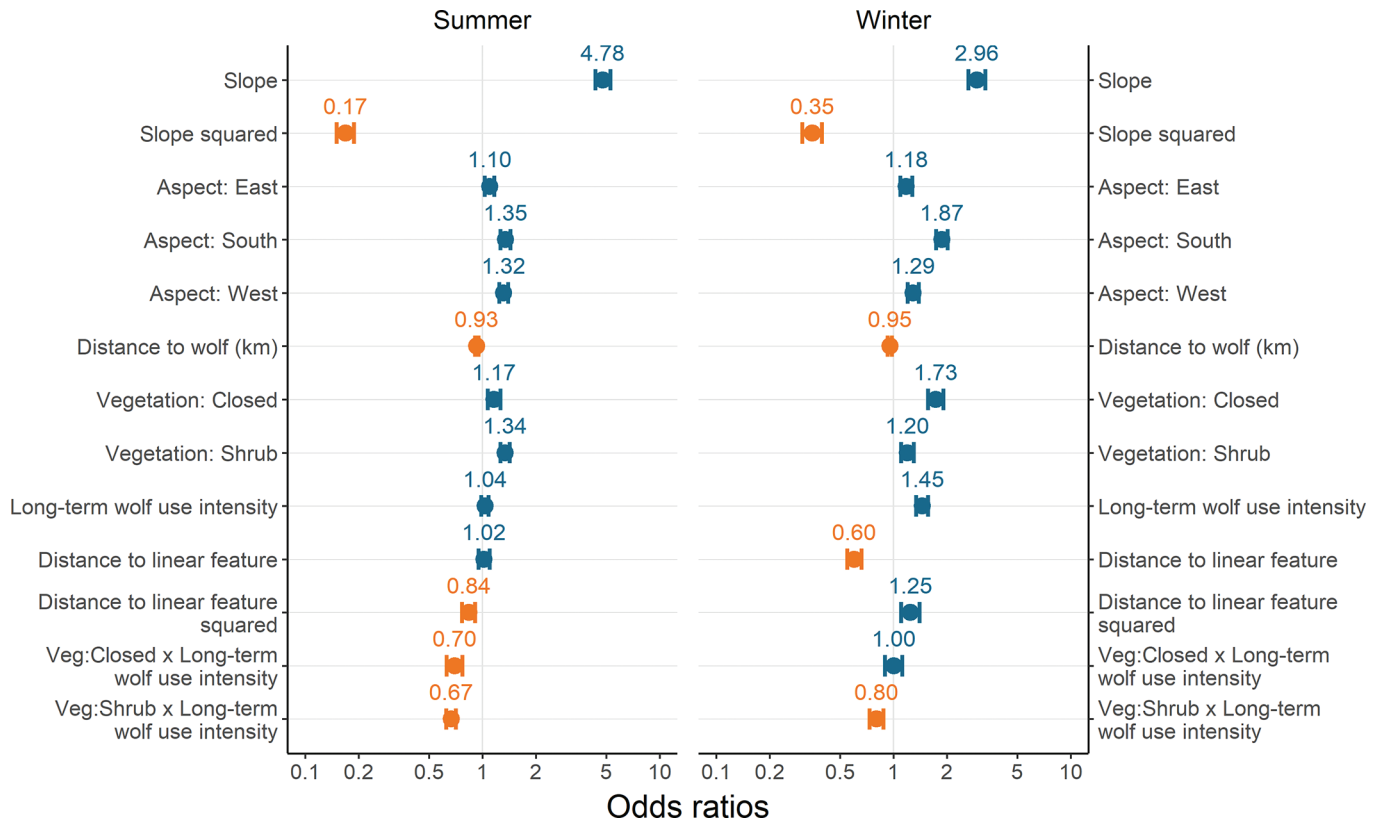
respond to wolf proximity, other studies of mesocarnivore risk responses have demonstrated primarily reactive risk mediation, suggesting that selection for prey availability or other metrics of habitat quality supersede the risk (or reward) of large carnivores except when they are actually nearby (Broekhuis et al. 2013; López-Bao et al. 2016; Balme et al. 2017).

There are several reasons why coyotes could be spatially associating with wolves. The opportunity to scavenge could be a strong draw, especially in wintertime, and might explain the attraction of coyotes to wolves and to areas of high wolf use during this season (Switalski 2003; Merkle et al. 2009). Previous studies in Alaska have shown high levels of carrion in coyote diets (Prugh 2005; Sivy et al. 2017a). Alternatively, coyotes and wolves may be selecting for similar environmental factors. For example, travel through snow can strongly affect energetics, and wolves and coyotes may therefore prefer areas with similar snow characteristics (Parker et al. 1984; Fancy and White 1987). This hypothesis is supported by the preference of coyotes for south-facing slopes, which would have the lowest mean snow load, and their preference for linear features, which represent common travel routes (Varhola et al. 2010). Because we did not have spatially and temporally explicit snow depth covariates or ground-validated wolf-kill locations, we cannot distinguish among these possibilities. However, given that both wolf-caused mortalities in our study occurred during winter, this positive spatial association may increase intraguild mortality risk for coyotes. Additional research is needed to determine whether this risk may be offset by acquisition of wolf-provided carrion. Our results also indicate that in open areas, particularly in the summer, coyotes may not react as strongly to either long-term or short-term wolf risk, suggesting that densely vegetated areas may be perceived as riskier by coyotes, despite the higher relative selection values of those vegetation types. This also suggests a potential risk trade-off when desirable linear features pass through closed vegetation, which could be tested in future analyses. Coyote home ranges were not restricted to the edges of wolf territories; a risk-avoidance method that has previously been hypothesized and reported for coyotes (Arjo and Pletscher 1999).

To our knowledge, our home-range estimates (mean  $291 \text{ km}^2$ , range  $57\text{--}1363 \text{ km}^2$ ) include the largest ever reported for coyotes. They are larger than home-range sizes reported for other coyotes in Alaska: Thurber (1992) found a mean minimum convex polygon (MCP) home range of  $87 \text{ km}^2$ , with one high outlier of  $236 \text{ km}^2$ , and Arthur (2003) found a mean MCP home range of  $118 \text{ km}^2$  during a snowshoe hare peak, although territories in areas without Dall's sheep averaged  $193 \text{ km}^2$ . For comparison, coyote territories in Utah, USA, and Idaho, USA, were no larger than  $40 \text{ km}^2$ , on average, even during periods of low resource availability, and those in Texas, USA, were a mere  $4 \text{ km}^2$  (Mills and Knowlton 1991; Gifford et al. 2017). While increasing fix rate can increase home-range size across different methods of size calculation (Arthur and Schwartz 1999; Girard et al. 2002; Mills et al. 2006), our home-range estimates were not sensitive to fix rate (for further discussion of home-range size and comparison of methods see the Home-range size section of the Supplementary material).<sup>1</sup> Our finding is in accordance with evidence suggesting that carnivore territories are generally larger at higher latitudes, and that this effect, as in other species, is driven by lower resource availability (Gompper and Gittleman 1991; South 1999; Withey and Marzluff 2009; Wilson and Shivik 2011).

The mean annual survival of coyotes reported here (0.50) is lower than other studies in Alaska (Thurber 1992; Prugh et al. 2005), and on the low end compared with survival rates for adult coyotes documented in populations at lower latitudes, which typically range from 0.60 to 1.0 (e.g., Bekoff 1977; Chamberlain and Leopold 2001; Gese 2001, 2005; Berger and Gese 2007). Anthropogenic mortality was low (0.14), suggesting that low coyote survival

**Fig. 4.** Estimated coefficients, on the odds ratio scale, of resource selection functions for coyotes (*Canis latrans*) in Denali National Park and Preserve, Alaska, USA, in summer (April–September) and winter (October–March). Error bars show percentile 95% confidence intervals. Blue denotes odds ratios greater than one, indicating an increase in selection associated with that parameter; orange indicates the reverse. Distances are in kilometres. Slope and distance values have been scaled and centered, scaled units are as follows. Summer: slope 11.6°; distance to linear feature 0.8 km; distance to nearest wolf (*Canis lupus*) 8.5 km. Winter: slope 11.5°; distance to linear feature 0.8 km; distance to nearest wolf 8.3 km. Color version online.



was not driven by exploitation. Instead, mortality from large carnivores was the leading cause of death, reinforcing the demonstrated risk posed by large carnivores. This study focused on adult resident coyotes, and the spatial and demographic effects of large carnivores could differ for other age and residency classes (Atwood and Gese 2008, 2010). Additional information on the spatial dimension of coyote mortality would help to better understand the link between the risk of predation from large carnivores and the associated fear effects (i.e., costs of antipredatory behavior; Prugh et al. 2019). The small sample size of this study limits the scope of analysis and inference, and additional work with larger samples are needed to extend the applicability of these findings.

As with any RSF approach, we made assumptions about “availability” that may not be supported (Kertson and Marzluff 2011). The sampling resolution of our data precluded a movement-based or utilization–distribution-based evaluation of resource use, but using such techniques on data of a finer resolution is recommended for future work. In addition, both metrics of wolf risk in our analysis accounted only for the locations of collared wolves and the individuals with them. Transient wolves, which are estimated to comprise approximately 10% of the population, and subgroups that split off from the pack may have added wolf risk to the landscape that we were unable to capture (Mech et al. 1998; Benson and Patterson 2015). Finally, the presence of bears on the landscape in summer likely represents a second important source of risk to coyotes, as well as affecting scavenging availability, since bears tend to monopolize carcasses and might

reduce the opportunities for scavenging by coyotes (Tallian et al. 2017).

Despite these limitations, our study provides new insights into the ecology of high-latitude coyotes that are relevant to conservation and management. Northern environments are challenging for coyotes — the combination of limited prey resources, harsh abiotic conditions, and interspecific killing result in low density and low survival. Coyotes did not universally avoid the risk of wolves; instead, they leveraged variation in wolf risk associated with seasonality, and potentially landscape features, to take advantage of limited resources. Our study indicates that apex-mesopredator coexistence may be facilitated by behavioral patterns that vary considerably in space and time. Expanding populations of other mesocarnivores, such as golden jackals (*Canis aureus* Linnaeus, 1758), red foxes, and raccoons (*Procyon lotor* (Linnaeus, 1758)) (Larivière 2004; Berteaux et al. 2015; Mori et al. 2015; Norén et al. 2015; Sokolov et al. 2016; Krofel et al. 2017; Salgado 2018), may use similar risk mediation strategies to colonize and persist in novel environments.

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