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Coyote (*Canis latrans*) diet and spatial co-occurrence with woodland caribou (*Rangifer tarandus caribou*)

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Abstract: The interplay of predator encounters and antipredator responses is an integral part of understanding predator–prey interactions and spatial co-occurrence and avoidance can elucidate these interactions. We conducted hard-part dietary analysis of coyotes (*Canis latrans* Say, 1823) and space use of coyotes and woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) to test two competing hypotheses about coyote and caribou predator–prey spatial dynamics using resource selection functions. The high encounter hypothesis predicts that coyotes would maximize encounters with caribou via high spatial co-occurrence, whereas the predator stealth hypothesis predicts that through low spatial co-occurrence with caribou, coyotes act as stealth predators by avoiding habitats that caribou typically select. Our dietary analysis revealed that ~46% of sampled coyote diet is composed of caribou. We found that coyote share space with caribou in lichen-barren habitat in both summer and winter and that coyotes co-occur with caribou in forested habitat during summer, but not during winter. Our findings support predictions associated with the high encounter predator hypothesis whereby coyotes and caribou have high spatial co-occurrence promoting caribou in coyote diet.

Key words: Canis latrans, coyote, diet analysis, predator–prey interactions, *Rangifer tarandus caribou*, resource selection function, stealth predators, woodland caribou.

Résumé : La compréhension de l'influence réciproque des rencontres de prédateurs et des réactions anti-prédation est essentielle à la compréhension des interactions prédateurs–proies, les motifs spatiaux de cooccurrence et d'évitement pouvant permettre d'élucider ces interactions. Nous avons réalisé une analyse des éléments durs de l'alimentation de coyotes (*Canis latrans* Say, 1823) et de l'utilisation de l'espace par les coyotes et les caribous des bois (*Rangifer tarandus caribou* (Gmelin, 1788)), dans le but de valider deux hypothèses concurrentes concernant la dynamique spatiale des interactions prédateurs–proies des coyotes et des caribous, en utilisant des fonctions de sélection de ressources. L'hypothèse des rencontres fréquentes prédit que les coyotes maximiseraient les rencontres de caribous par l'entremise d'une forte cooccurrence spatiale, alors que l'hypothèse de la furtivité des prédateurs prédit que, par une faible cooccurrence spatiale avec les caribous, les coyotes se comportent comme des prédateurs furtifs en évitant les habitats typiquement sélectionnés par les caribous. Notre analyse de régimes alimentaires révèle que ~46 % des régimes alimentaires de coyote échantillonnés comprennent du caribou. Nous observons que les coyotes partagent l'espace avec des caribous dans des habitats de toundra à lichen en été comme en hiver et qu'il y a cooccurrence de coyotes et de caribous dans des habitats forestiers en été, mais pas en hiver. Nos constatations appuient les prédictions associées à l'hypothèse des rencontres fréquentes de prédateurs selon laquelle la cooccurrence spatiale des coyotes et des caribous est forte, favorisant la présence de caribous dans l'alimentation des coyotes. [Traduit par la Rédaction]

Mots-clés : Canis latrans, coyote, analyste du régime alimentaire, interactions prédateurs–proies, *Rangifer tarandus caribou*, fonction de sélection de ressources, prédateurs furtifs, caribou des bois.

Introduction

Encounter rates of predators with prey are an integral component of predator–prey dynamics (Brown et al. 1999; Brown 1999). The shared space use of a predator and their prey can approximate encounter rates, as sharing space is a prerequisite for encounters (Hebblewhite et al. 2005; Waddle et al. 2010; Bastille-Rousseau et al. 2016*a*; Watters et al. 2018). Generally, predators achieve high capture success through high encounter rates (Brown et al. 1999). However, increased encounters can lead to learned vigilance by prey (Brown 1999; Lima 2002). Simulations predict that predators are most successful when maximizing encounters but also minimizing spatial overlap so as not to alert prey species of their presence (Brown et al. 1999; Brown and Kotler 2004; Sih et al. 2010)

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Table 1. Research describing the predator–prey relationship of coyote (*Canis latrans*) and prey species using dietary analysis on the Island of Newfoundland, Canada.

			Prey			
Study	Season	Measurement unit	Rank 1	Rank 2	Rank 3	Rank 4
Bridger 2005	Winter	% Occurrence	Caribou	Hare	—	—
McCue 2012	Summer	% Occurrence	Bird (14.35%)	Vole (13.43%)	Hare (12.96%)	Caribou (11.11%)
	Summer	Estimated mass (g)	Caribou (224.91)	Hare (212.69)	Bird (136.09)	Vole (60.20)
Mumma et al. 2016	Summer	% Occurrence (morphological)	Hare*	Moose*	Caribou	—
	Summer	% Occurrence (molecular)	Moose	Hare	Caribou	—
Zieminski 2016	Summer	% Occurrence	Hare (57.0%)	Caribou (46.1%)	Moose (33.3%)	Beaver (8.2%)
This study	Summer	% Occurrence	Caribou (45.7%)	Hare (25.9%)	Vole (22.4%)	Plant (15.5%)

Note: For our study, we collected scat in summer, but we were unable to determine the age of scat samples. Asterisks denote prey species that are approximately equally represented in coyote diet.

High encounter rates by predators may be driven by habitat selection of predators. For example, wolves (*Canis lupus* Linnaeus, 1758) select habitat that is associated with high prey densities (Kittle et al. 2017). The high encounter hypothesis predicts that predators exhibit similar patterns of habitat selection to their prey, thus resulting in high spatial co-occurrence with prey.

Predator–prey relationships are highly dynamic, and whereas predators aim to co-occur with prey, prey typically display various morphological and behavioural traits that offset encounters with predators. For example, some prey may be larger or more dangerous, traits that could attenuate the benefits of high co-occurrence because of the potential for injury and wasted energy. Moreover, traits that improve prey antipredator responses such as vigilance may further decrease predator kill rates (Middleton et al. 2013). Thus, some predators may use alternative space use strategies to appear to limit antipredator behaviour of prey. For example, cougars (*Puma concolor* (Linnaeus, 1771)) select different habitat than mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), exploiting prey awareness of predators, described as a predator stealth strategy (Laundré 2010). Furthermore, seasonal variation in prey traits, including body condition or reproduction status, may also affect vulnerability on potential mechanisms explaining variation in predator–prey encounter rates (Bastille-Rousseau et al. 2016*b*; Bonar et al. 2018; Gulsby et al. 2018; Viejou et al. 2018).

Coyotes (*Canis latrans* Say, 1823) are widely described as generalist predators (Andelt et al. 1987; Gompper 2002; Dowd and Gese 2012; McCue et al. 2014). Coyotes have expanded their range across North America and have adapted feeding strategies to profit from various locally abundant prey species, including ungulates (Prugh et al. 2009; Ellington and Murray 2015). As a recent invader to the Island of Newfoundland, coyotes have encountered woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788); henceforth caribou) as prey. Consumption of caribou by coyotes is well documented in Newfoundland (Table 1) and in some areas of Quebec (Crête and Desrosiers 1995; Boisjoly et al. 2010), although the majority of predation events are of neonate caribou (Lewis and Mahoney 2014). Coyotes also hunt and kill large, adult, ungulate prey including moose (*Alces alces* (Linnaeus, 1758)) (Benson and Patterson 2013), mule deer, and elk (*Cervus canadensis* Linnaeus, 1758) (Dowd and Gese 2012). We therefore assume that coyotes are capable of hunting and killing adult caribou in Newfoundland (see Lewis and Mahoney 2014). Caribou, like other adult ungulates, pose an injury risk to coyotes during encounters (Berger 1979; Mukherjee and Heithaus 2013; Brown et al. 2016). Despite this risk, coyotes may target large prey due to higher energetic gains. For example, coyotes prefer to consume white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) over snowshoe hare (*Lepus americanus* Erxleben, 1777) despite high hare availability (Patterson et al. 1998). In the absence of competing predators, coyotes in West Virginia (USA) are the top predator for white-tailed deer (Crimmins et al. 2012). Coyotes may therefore employ spatiotemporal hunting strategies to increase the likelihood of capturing larger prey, which can be tested by examining patterns of co-occurrence between coyotes and larger prey species.

Here, we collected coyote scat samples and infer habitat selection based on the locations of scat samples and contextualize the co-occurrence between coyotes (a generalist predator) and caribou (a large and therefore energetically profitable prey species). We estimated the presence and frequency of different prey items in coyote diet. We predicted that, regardless of predation strategy, caribou would consist of the greatest frequency of prey in coyote diet because the energetic profitability of large prey is an incentive for coyotes to prioritize caribou as prey. We then estimated habitat selection using resource selection functions (RSFs) for GPS-collared caribou, as well as diet-specific RSFs for coyotes, and tested the high encounter and predator stealth hypotheses:

1. The high encounter hypothesis predicts that coyotes with caribou in their diet would select for the same habitats as caribou. Coyote resource selection would therefore be similar to that of caribou, selecting and avoiding similar habitats in both summer and winter. By contrast, the predator stealth hypothesis predicts that coyotes with caribou in their diet would not select for the same habitat as caribou to reduce encounters with caribou and therefore impose a false sense of security that would reduce caribou vigilance and increase capture success (Brown 1999; Lima 2002; Sih et al. 2010).
2. The high encounter hypothesis predicts that coyotes that have caribou in their diet will have similar patterns of resource selection to caribou compared with coyotes that do not consume caribou. Given limited spatial co-occurrence between caribou and coyotes, we predict either no relationship between caribou resource selection and coyote diet or dissimilarity in co-occurrence where caribou avoid areas where they also appear more in the diet of coyotes. By contrast, the predator stealth hypothesis predicts either no relationship between caribou resource selection and coyote diet or dissimilarity in co-occurrence where caribou avoid areas where they also appear more in the diet of coyotes.
3. The high encounter hypothesis predicts no variation in probability of co-occurrence between caribou in either summer or winter and coyotes that either consume, or do not consume, caribou because coyotes do not attenuate their encounter rates with caribou. By contrast, the predator stealth hypothesis predicts the probability of spatial co-occurrence would be higher in summer compared with winter because adult caribou are more vulnerable to predation in winter due to low energy reserves as a result of food limitation (Schaefer et al. 2016).

Materials and methods

Study area and species

We investigated the predator–prey dynamics of caribou and coyotes on Fogo Island (49°40′00″N, 54°11′00″W), Newfoundland

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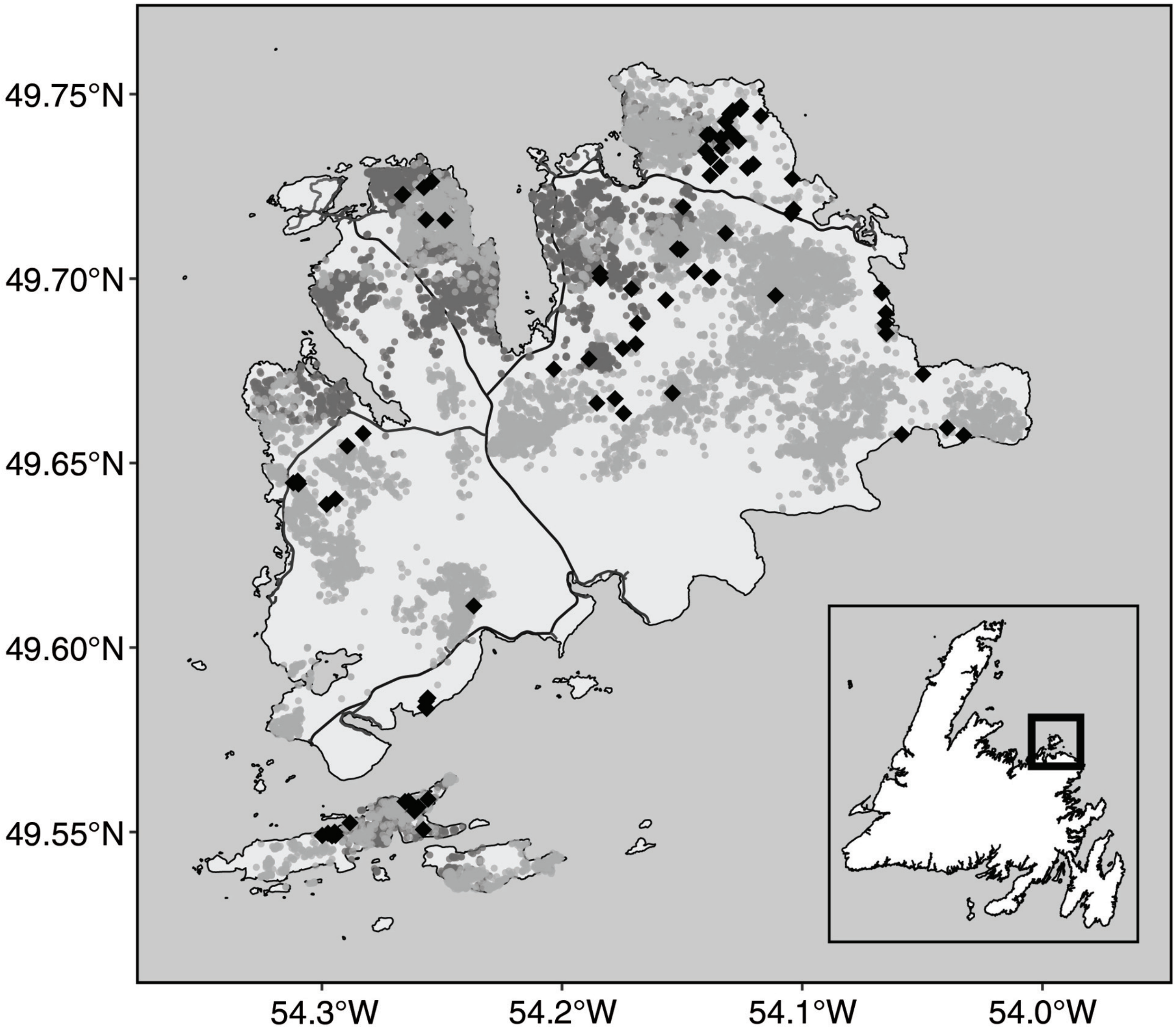
Fig. 1. Map of the Fogo Island study area with inset showing the extent of the Island of Newfoundland, Canada. Locations of coyote (*Canis latrans*) scat are represented by large black diamonds, woodland caribou (*Rangifer tarandus caribou*) GPS locations in winter are represented by dark grey dots, and caribou summer GPS locations are represented by light grey dots. Roads are represented by black lines. Base map of Fogo Island and the Island of Newfoundland from the R package "osmdata" (Padgham et al. 2017) via the open source platform OpenStreetMap (available from https://www.openstreetmap.org/#map=2/71.3/-96.8).



and Labrador (hereafter Newfoundland), Canada (Fig. 1). Fogo Island is a small (238 km^2) island off the northeastern coast of Newfoundland and has a humid climate with year-round precipitation. Primary habitat types include mixed-wood and conifer forests composed of balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.), tamarack (*Larix laricina* (Du Roi) K. Koch), and white birch (*Betula papyrifera* Marshall). Other habitat types include ponds, bog wetlands, lichen, and rocky barrens.

Novel to the Island of Newfoundland, coyotes arrived from Cape Breton, Nova Scotia, Canada, by crossing sea ice in approximately 1985 (McGrath 2004). The first trapped coyote specimen from Fogo Island was submitted to the Newfoundland and Labrador Wildlife Division in April 2008 (Newfoundland and Labrador Wildlife Division, unpublished data); however, coyotes likely colonized Fogo Island prior to 2008. Free of black bears (*Ursus americanus* Pallas, 1780) and wolves, coyotes are the apex predator on Fogo Island. Although coyotes have been present on Fogo Island since at least 2008, their density remains unknown. Based on home-range sizes for coyotes in Newfoundland and throughout their range (Ellington and Murray 2015), it is possible that Fogo Island could host as few as one (assuming an upper limit of 300 km^2 home ranges), but as many as seven (assuming a lower limit of ~35 km^2 home ranges), breeding pairs of coyotes.

Caribou GPS telemetry data

Adult female caribou were fitted with on-board storage GPS radio collars (1240 g, GPS 4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada). Live captures consisted of helicopter captures using the immobilizing agent carfentanil, delivered via dart gun and carried out by the Newfoundland and Labrador Wildlife Division in spring 2016 (n = 15) and 2017 (n = 14). Collars were programmed to collect location fixes every 2 h between 12 April 2016 and 3 March 2018. We processed telemetry data to remove outliers following Bjørneraas et al. (2010). In addition, we assumed all caribou locations recorded in the ocean were erroneous and therefore excluded them from subsequent analyses. We also removed all locations that occurred over freshwater lakes or streams because we did not collect coyote scat in these areas and

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our goal was to directly compare caribou and coyote habitat selection. After processing and restricting data to only summer and winter (see below), our dataset contained 37 370 caribou locations. All animal capture and handling procedures were consistent with the American Society of Mammologists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and were approved by Memorial University Animal Care and Use Committee (16-03-EV).

Coyote scat collection and processing

Dietary information of Fogo Island coyotes was derived from fecal samples (scat) that were collected opportunistically by observers in the field. For each scat sample collected in the field, the GPS location was recorded, and the sample was frozen at −20 °C until processing. In addition to the scat locations, we recorded the daily tracks of human observers (hereafter, daily observer track) using handheld GPS devices (Garmin GPSMAP® 64st). Daily observer tracks represented the entire route walked by a field team on a given day. Tracks represent the areas where observers could have encountered and collected scat and we collected, on average, 2.3 scat samples per daily observer track. During spatial data cleaning, scat samples that were not associated with a daily observer track were eliminated from spatial analysis but were retained for dietary analyses. In total we collected 116 coyote scat samples between spring 2016 and autumn 2018. Spatial data from 20 samples were not recorded, resulting in 96 locations for spatial analyses (see below). To process scat samples for dietary analysis, they were first dehydrated in an oven at >85 °C for 7 days. Dried samples were then placed in a fine strainer and washed under warm water to mechanically separate digested material from undigested animal or plant remains, or hard parts, e.g., hair, feathers, bones, teeth, and seeds. Hard parts were then air-dried for an additional 7 days. Our spatial analyses using the locations of scats may have been biased to areas where scat were more visible and where coyotes are more likely to deposit scat (for assumptions and caveats see Supplementary Table S1).[1] Despite this, our coyote spatial analyses (see below) were qualitatively similar to analyses conducted based on coyote locations generated from GPS-collar data in Newfoundland (McCue et al. 2014; Bastille-Rousseau et al. 2015; Ellington 2016).

Coyote diet and frequency analysis

Coyote diet was determined using hard-part analysis via the identification of hair extracted from scat samples. We used compound light microscopy to identify mammalian prey items based on hair medulla structure and macrolevel physical qualities following the Alaska Fur ID Project (Carrlee 2010). Additional identifications were made via comparative analysis of reference hair samples taken from known species provided by Memorial University of Newfoundland collections. A given prey species was considered present in a scat sample if the hair type extracted composed greater than 5% of the total mass of undigested material (Klare et al. 2011). Non-mammalian samples were categorized broadly, i.e., plants and birds. We calculated the percentage of samples that contained each type of prey species (Supplementary Table S2).[1]

Spatial analysis: resource selection functions

We used resource selection functions (RSFs) to evaluate caribou and coyote space use (Manly et al. 2002; McLoughlin et al. 2010). RSFs use a logistic regression framework where used and available locations are compared to predict the relative probability of selection. Habitat variables were derived from Landsat 7 data containing eight habitat types at a resolution of 30 m × 30 m and elevation was extracted from a digital elevation map at 30 m × 30 m (Wulder and Nelson 2003). Habitat types included conifer scrub, wetland, rocky barrens, deciduous mixed woodland, conifer woodland, lichen barrens, water, and anthropogenic features (roads and buildings). We also used a digital elevation model to quantify elevation. Caribou RSFs were defined at the level of the study area, with available points being generated over all of Fogo Island (excluding water bodies) at a ratio of 5:1. Since we did not have GPS-collar data for coyotes, we used scat location as a proxy for coyote space use. Due to the relatively small sample size of coyote scat samples, we generated available points across Fogo Island at a ratio of 10:1 and used a permutation approach to generate selection coefficients. When generating available points for coyote RSFs, we retained the ratio of observed scat locations per daily observer track in the dataset. For example, if we collected two scat samples on a given daily observer track, we generated 20 available locations associated with that observer track. To decrease the potential of multicollinearity between habitat variables, we quantified the proportion of each habitat within a 100 m buffer of each used and available location. We used a 100 m buffer around available locations to capture potential heterogeneity in habitat types within a localized area and to reduce the potential for issues with multicollinearity in the analyses. Elevation values were scaled using maximum–minimum normalization over the range of values on Fogo Island (0–110 m) to be on the same scale as our habitat variables. Due to relatively small sample sizes for coyote data, we used a permutation approach to generate selection coefficients. We iteratively re-assigned available points and re-generated resource selection functions 500 times. This approach enabled us to have confidence that our comparison of observed and available locations were not biased by any given set of available locations. As a result, we generated distributions of 500 coefficient estimates (Supplementary Figs. S1 and S2),[1] their associated 95% confidence intervals (95% CIs) (Supplementary Figs. S3 and S4),[1] and the coefficient to 95% CI ratio (Supplementary Figs. S5 and S6).[1] The coefficient to 95% CI ratio is equivalent to an effect size to variance ratio, where values that exceed one represent a statistically plausible effect where the magnitude of the effect size exceeds the variance associated with the effect.

To estimate seasonal variation in caribou RSFs, we subset caribou location data into winter (15 January to 3 March; n = 17 456) and summer (15 July to 1 September; n = 19 914). We based these temporal extents on the presence or absence of snow cover across the landscape. The presence of snow during the winter restricts access to vegetation, whereas the absence of snow during summer results in a relatively homogeneous distribution of vegetation. To determine whether there was variation in coyote space use based on diet, we subset coyote data based on presence (n = 46) or absence (n = 50) of caribou in the diet. Because we were unable to determine the exact date coyote scat samples were deposited, we did not separate coyote data into temporal subsets.

Spatial analysis, model selection, and validation

Our goal was to compare resource selection across species and contexts, i.e., season for caribou and dietary type for coyote. We therefore generated a single global model for all four analyses using five habitat types (wetland, forest, conifer scrub, rocky barrens, and lichen barrens) and elevation. We excluded water and anthropogenic land-cover classes from the models because we did not collect coyote scat on frozen lakes in winter, along roads, or immediately adjacent to anthropogenic features. In addition, we combined coniferous, deciduous, and mixed-wood forest habitat types into a single forest variable for subsequent analysis.

For each of the four models, we used generalized linear mixed-effects models that were parameterized with a binomial error distribution. For the caribou RSFs, we included individual identity as a random effect (Gillies et al. 2006), and for coyote RSFs, we included daily observer track as a random intercept. We tested

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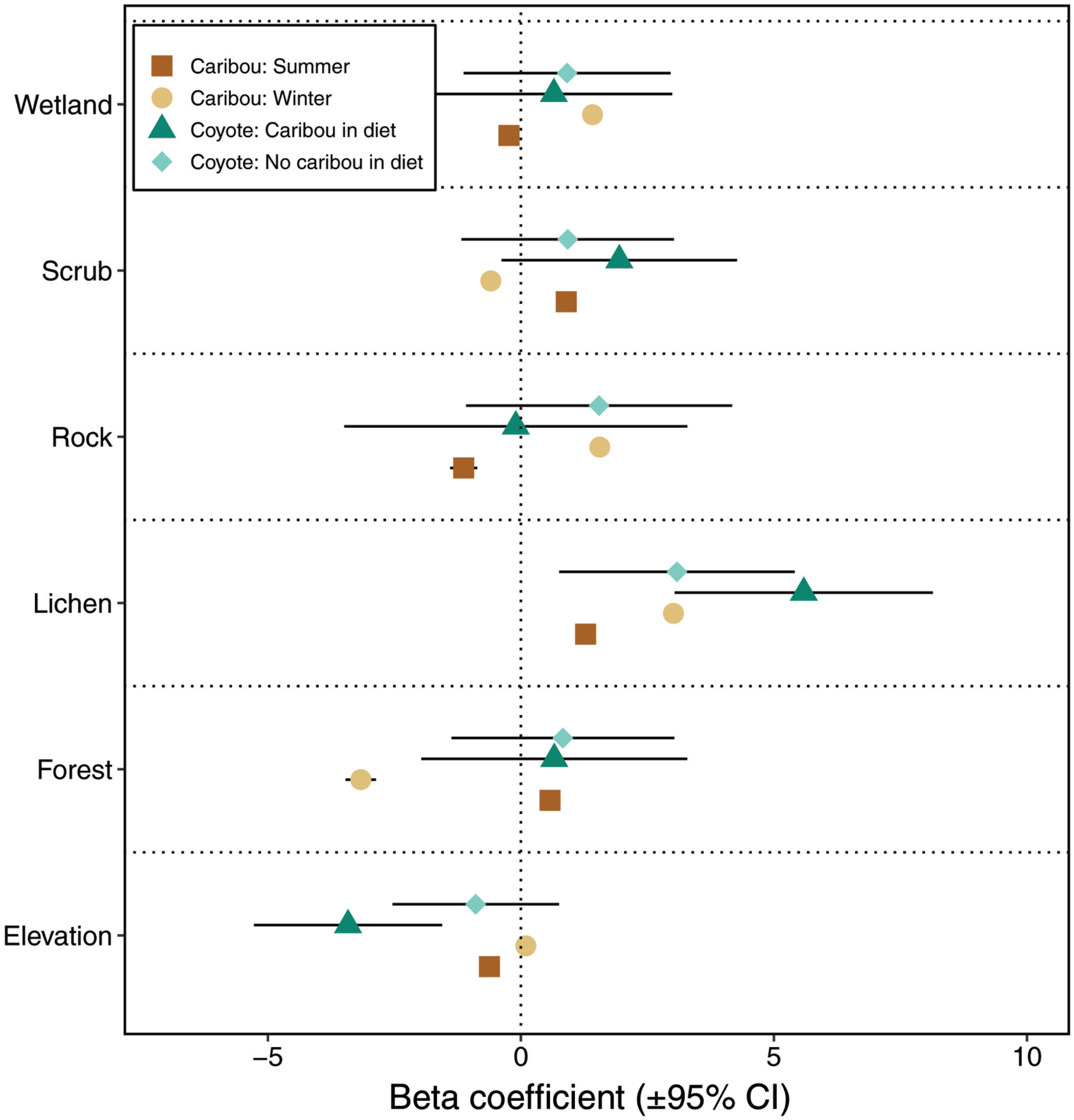
[1] Supplementary tables and figures are available with the article at https://doi.org/10.1139/cjz-2020-0253.

Fig. 2. Habitat selection coefficients (*x* axis) for five habitat types and elevation (*y* axis) for woodland caribou (*Rangifer tarandus caribou*; *n* = 29) in winter and summer, as well as for coyote (*Canis latrans*) scat samples that were found to contain caribou and those that did not. The vertical dotted line represents a beta value of 0, i.e., neither selection nor avoidance, and the horizontal dotted lines separate habitat types. Solid horizontal lines around each point indicates 95% confidence intervals (95% CIs). We generated 95% CI for coyote beta coefficients based on the distribution of coefficients extracted from 500 permutations of available points. Note that 95% CI for caribou data are very small and may be hidden by symbols. Colour version online.



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for collinearity among variables using variance inflation factors (VIFs) and ensured that all covariates had a VIF < 4 (O'Brien 2007). To infer potential spatial co-occurrence relationships between caribou and coyotes, caribou RSFs and coyote RSFs were compared. We assumed that similar positive selection coefficients for a given covariate represents high probability of spatial co-occurrence, whereas selection coefficients with opposing signs for a given habitat variable represents a low probability of spatial co-occurrence.

We evaluated the predictive performance of our models using *k*-fold cross validation (Boyce et al. 2002; Roberts et al. 2017). This was performed by training the model with 80% of the data and testing the predictive performance with the remaining 20% by evaluating whether there is a positive correlation in the proportion of locations that were used, compared with the available sample, and RSF score bin (deciles of predicted RSF scores). Positive correlations therefore indicate increasing relative use in the test sample as a function of predicted values from the model fit using the training data. This was performed five times, withholding a different 20% for testing each time, and the mean and SD are presented. For the caribou models, folds were divided based on animal ID; for the coyote models, we used transect ID to assort into individual folds.

Results

Dietary analysis

From a total of 116 scat samples, we found, on average, 1.45 prey items per sample. We identified specimens from eight mammal species or taxa (caribou, hare, vole, seal, beaver, mustelid, murid or sciurid, and moose), as well as birds and plants (Supplementary Table S2).[1] The most common prey found in coyote diet was caribou, which occurred in 45.7% (*n* = 53/116) of all scat samples (Table 1). Hare occurred in 25.9% (*n* = 30/116) of all scat samples, whereas vole was found in 22.4% (*n* = 26/116) of scat samples. Coyote diet also contained

Table 2. Summary of resource selection beta coefficients (±95% confidence intervals) of woodland caribou (*Rangifer tarandus caribou*; n = 29) in summer and winter and coyotes (*Canis latrans*) with caribou in their scat (n = 46 scat locations) and coyotes without caribou in their scat (n = 50 scat locations).

	Caribou		Coyote scat	
Variable	Summer	Winter	Contained caribou	Did not contain caribou
Intercept	−1.79 (−1.96, −1.62)	−3.06 (−3.84, −2.29)	−2.97 (−4.80, −1.15)	−3.16 (−4.85, −1.51)
Wetland	−0.24 (−0.34, −0.13)	1.41 (1.31, 1.52)	0.65 (−1.68, 1.68)	0.89 (−1.13, 2.96)
Conifer scrub	0.90 (0.80, 0.99)	−0.59 (−0.72, −0.47)	1.94 (−0.38, 4.26)	0.91 (−1.18, 3.02)
Rock barrens	−1.13 (−1.31, −0.95)	1.56 (1.43, 1.69)	−0.10 (−3.49, −3.28)	1.53 (−1.08, 4.17)
Forest	0.57 (0.47, 0.67)	−3.16 (−3.36, −2.96)	0.66 (−1.97, 3.29)	0.82 (−1.37, 3.03)
Lichen barrens	1.27 (1.15, 1.40)	3.01 (2.89, 3.14)	5.59 (3.03, 8.14)	3.05 (0.75, 5.41)
Elevation	−0.62 (−0.71, −0.53)	0.10 (−0.05, 0.25)	−3.42 (−5.27, −1.56)	−0.91 (−2.54, 0.75)

plant materials, which was found in 15.5% (n = 18/116) of scat samples, and seal, which comprised 11.2% (n = 13/116) of scat samples (Supplementary Table S2).[1]

Caribou resource selection functions

Habitat selection in caribou remained consistent across seasons for some habitat types but varied in others. During both summer and winter, caribou selected for lichen barrens. Caribou selected rocky barrens and wetland in winter but avoided these habitats during the summer (Fig. 2; Table 2). By contrast, caribou selected forest and conifer scrub in summer but avoided these habitats in winter (Fig. 2; Table 2). We also detected a seasonal shift in selection for elevation, with caribou selecting for areas at higher elevation in the winter compared with in the summer (Fig. 2; Table 2). Our caribou RSF models had a moderate k-fold cross-validation score in the summer of $\rho = 0.19$ (0.57 (±SE)) and a strong k-fold cross-validation score in the winter of $\rho = 0.95$ (0.06).

Coyote resource selection functions

Patterns of habitat selection for coyotes inferred from scat were similar for scat that contained caribou and scat that did not contain caribou. Given our small sample size for our coyote data, we had relatively large confidence intervals around our habitat selection coefficients, so we cautiously interpret coefficients from these models. Our models highlight that coyotes with caribou in their scat, and those without caribou in their scat, selected for lichen barrens and forest (Fig. 2; Table 2). Meanwhile, for both models, i.e., coyotes with caribou in their scat and coyotes without caribou in their scat, there was marginal selection for wetland, conifer scrub, and forest (Fig. 2; Table 2). Coyotes with caribou in their scat selected rocky barrens, whereas coyotes with caribou in their scat neither selected nor avoided rocky barrens (Fig. 2; Table 2). Avoidance of elevation was similar for both coyotes with and without caribou in their scat, although avoidance was stronger for coyotes that had caribou in their scat (Fig. 2; Table 2). For coyotes with caribou in their scat, $\rho = 0.47$ (0.11), which given our sample size represented a reasonably good outcome. By contrast, for coyotes without caribou in their scat, $\rho = 0.07$ (0.60), which represents a relatively poorly performing model. Logically, our hypotheses were aimed at comparing space use of caribou and coyotes with caribou in their scat, and thus coyote that consumed caribou, therefore highlighting that the poor performance of the model for coyotes without caribou in their scat does not affect our conclusions.

Predator–prey spatial co-occurrence

Spatial co-occurrence between coyote scat that contained caribou and caribou was most likely to occur in open habitats and less likely in closed habitats. Meanwhile, coyotes that contained, and did not contain, caribou in their diet selected forests in summer and winter, whereas caribou selected forests only in summer. In both summer and winter, the probability of co-occurrence was greatest between caribou and coyote scat that contained caribou in lichen barrens (Fig. 2). By contrast, caribou and coyotes that contained, and did not contain, caribou in their diet had relatively low probability of co-occurrence in wetlands (Fig. 2).

Discussion

We found that coyotes generally had high spatial co-occurrence with caribou, presumably to maximize predation opportunities, and that caribou were their primary prey. The high encounter hypothesis posits that predators should co-occur with their prey to ensure that encounters, and subsequent kill rates, are as high as possible. High spatial co-occurrence can result in greater stress and reduced fecundity for prey and can therefore influence population dynamics (Say-Sallaz et al. 2019). In addition to spatial co-occurrence with caribou, we also found that approximately 50% of coyote scat samples contained caribou.

Coyotes consumed caribou as a primary prey item, which was consistent with the high encounter hypothesis. Throughout most of their range, there is limited evidence of a predator–prey relationship between coyotes and caribou (Latham et al. 2013), although other caribou herds in Newfoundland do experience high predation by coyotes on calves and occasionally adults (Lewis and Mahoney 2014; Bastille-Rousseau et al. 2016*a*; Lewis et al. 2017). On Fogo Island, coyotes are the only major predator of caribou. In areas where other predators co-occur with coyotes, e.g., wolves or bears, coyotes are typically outcompeted for ungulate prey (Newsome et al. 2017), interfered with or even consumed themselves (Berger and Gese 2007), and therefore are less likely to consume large prey. In the absence of competing predators, our results suggest that coyotes shift their predation habitats to focus on caribou as a primary prey source (Crimmins et al. 2012). In jurisdictions that cull wolves as a method to conserve caribou (Hervieux et al. 2015; Serrouya et al. 2019), coyotes could emerge as an alternative predator of caribou in the absence of wolves, reducing the effectiveness of predator control as a conservation tool. The observed shift from smaller prey to larger prey in the absence of competitors presumably occurs because ungulates are more energetically profitable than smaller alternative prey (Patterson et al. 1998) and the reduced risks associated with competition between predators.

Caribou selection varied seasonally within forested habitats. Caribou avoided forests in winter, possibly as a predator avoidance tactic because coyotes may select forested habitats (Murray et al. 1994) or because caribou rely so strongly on lichen habitats for food resources in winter (Brown and Theberge 1990; Fortin et al. 2008). However, caribou selected forest habitats during summer, presumably as a predator avoidance tactic for females with calves (Bergerud et al. 1990) and because foraging opportunities are available (Johnson et al. 2001; Hornseth and Rempel 2016), but also as a refuge from insect harassment (Raponi et al. 2018). Caribou clearly demonstrate seasonal changes in their selection of forest habitat and our findings are corroborated by past work suggesting that predator avoidance is an important reason why caribou select, or avoid, forest habitat (Basille et al. 2015; Bastille-Rousseau et al. 2018).

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Although we generally found support for the high encounter hypothesis, it is possible that coyotes remain inefficient predators of caribou and other ungulates. Coyotes may still limit encounters with caribou to reduce vigilance (Brown 1999; Lima 2002; Sih et al. 2010). It is possible that high encounter and predator stealth are non-mutually exclusive hypotheses and may be habitat specific. In our analysis, coyotes with caribou in their diet may avoid rocky barrens to prevent visual detection, especially during winter when caribou have greater selection for rocky barrens. This supports the predator stealth hypothesis where avoidance of rocky barrens may reduce vigilance in caribou. A potential phenomenon that influences whether coyotes adopt a high encounter or stealth strategy could be the local abundance of other prey, such as snowshoe hare. Given that snowshoe hare typically undergo population cycles in the boreal forest (Krebs et al. 1995), coyotes could switch between consuming primarily snowshoe hare and caribou, depending on hare density. Coyotes are known to switch prey between snowshoe hare and white-tailed deer, where deer consumption increased at low hare density (Patterson et al. 1998).

An important caveat of our study is the relatively small number of coyote locations inferred from the locations of collected scat samples (see Supplementary Table S1).[1] Although the model for coyote scat that did not contain caribou performed poorly in our cross-validation analysis, the model for coyote scat that contained caribou performed relatively well given the small sample size. In addition, the general results from these models indicate similar resource selection patterns for coyotes as studies which deployed GPS collars on coyotes in Newfoundland (McCue et al. 2014; Bastille-Rousseau et al. 2015; Ellington 2016). Despite these similarities, our coyote models should be interpreted with caution owing to limited sample size and because scat collection was opportunistic. In addition, our inability to determine the time that a scat was deposited resulted in aseasonal spatial analyses for coyotes. We therefore cautiously interpret models of coyote space use and note the benefit of using locations of scat samples is the ability to infer diet in addition to space use. Indeed, we were unable to associate the location of scat with locations where caribou were killed or consumed. Moreover, the gut passage time for coyotes is approximately 6 h (Weaver and Hoffman 1979), so it is likely that the location of scat collection was not the location of a kill.

An additional caveat is that we were unable to distinguish between adult and calf caribou hair in coyote scat samples (see Supplementary Table S1).[1] This is important because caribou calves are more vulnerable to coyote predation than adults (Rayl et al. 2014). The implications of this distinction are twofold. First, calves are most vulnerable during the first weeks of life and identifying calf hair could have helped separate coyote data into temporal subsets. Second, our inference about spatial co-occurrence was more limited than if we had estimated the difference in co-occurrence for coyote scat that contained adults or calves. Adult female caribou do not actively defend calves during predator encounters, suggesting that the predictions associated with the high encounter hypothesis should be supported for calf predation (Bastille-Rousseau et al. 2016*a*). In the context of biomass, coyotes consumed more caribou biomass than other species, which suggests it is unlikely that they only consumed calves during spring and early summer. Future studies should address seasonal variation in the composition of coyote diet, i.e., adults compared with calves, in conjunction with spatial co-occurrence. Additionally, individual variation in diet is a crucial consideration for future scat analysis to make inferences on spatial co-occurrence with prey species. Molecular analysis and mark–capture–recapture methods could be used to determine individual variation in diet, an approach which would be particularly relevant due to the geographical constraints on the maximum number of coyote territories that could be found on Fogo Island (Ellington 2016). Scavenging on caribou may be an alternative explanation to the presence of caribou in coyote diet and may require further investigation. However, scavenging by coyotes is often the result of coyotes scavenging at the kill sites of sympatric predators (Wilmers et al. 2003; Atwood and Gese 2008), of which there are none on Fogo Island. Therefore, although it is possible that coyotes scavenged on caribou that died from injury or illness, scavenging likely does not account for a large proportion of caribou in coyote diet.

Across their range, caribou (*Rangifer tarandus* (Linnaeus, 1758)) are undergoing declines (Festa-Bianchet et al. 2011; Mallory and Boyce 2018). Although some declines have been attributed to human-mediated predation (Wittmer et al. 2005; Johnson et al. 2019), we suspect that the predator–prey relationship between coyotes and woodland caribou on Fogo Island, and potentially other parts of Newfoundland, may not be related to human activity. Specifically, coyotes are relatively new predators of woodland caribou, but in the absence of wolves, they appear to display behavioural and foraging flexibility to hunt and consume woodland caribou. In the absence of wolves, coyotes may experience mesopredator release, such that coyotes are free from spatial or dietary suppression associated with competition with wolves (Newsome et al. 2017). Our study adds to the existing work on caribou–coyote interactions, and through a combination of dietary and spatial analyses, we demonstrate the complex spatial relationship between coyotes and caribou.

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