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The Role of Predation in Woodland Caribou Population Declines in Northeastern Alberta – Coyotes

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A. David M. Latham[1, 2], M. Cecilia Latham, Mark S. Boyce, and Stan Boutin

Department of Biological Sciences, CW405, Biological Sciences Building, University of Alberta, Edmonton, Alberta, T6G 2E9

[1] Corresponding author: LathamD@landcareresearch.co.nz
[2] Present address: Landcare Research, PO Box 40, Lincoln 7640, Canterbury, New Zealand.

Abstract

Coyote (*Canis latrans*) range extension has been generally associated with the expanding frontiers of human activity and footprint; however, little is known about coyote expansion into the boreal forest, their interactions with sympatric wolves (*C. lupus*) or their potential role as predators of calves of threatened woodland caribou (*Rangifer tarandus caribou*). We assessed coyote habitat selection, diet, and spatiotemporal relationships with caribou, wolves, and industry in a caribou range in northeastern Alberta, Canada. Our results support the hypothesis that industrial footprint has facilitated coyote range expansion into caribou range. Coyotes and wolves showed resource partitioning, with coyotes specializing on small prey and wolves specializing on moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and beaver (*Castor canadensis*). Deer was also common in coyote diet, suggesting this prey species might be contributing to the northward range expansion of coyotes. During the caribou calving season, wolves avoided caribou-preferred habitats (i.e., bogs and fens); however, 2 packs diverged from this pattern by showing selection for fens. Conversely, the 4 coyotes we assessed showed selection for bogs or fens. These results suggest both canid predators spend time foraging in areas frequented by caribou. However, scat analyses revealed that caribou were rare in coyote diet, a phenomenon also reported for wolves. Because even limited predation on caribou adults and calves can have a significant impact on caribou populations, we recommend that management actions to conserve caribou should focus on alternative predators in addition to wolves.

Introduction

Coyotes (*Canis latrans*) were historically restricted to the Great Plains of Midwestern and western United States (Young and Jackson 1951; Parker 1995; Gompper 2002). In the past 2 centuries coyotes expanded their range to include much of North America, including the entire eastern seaboard, south into Mexico and Central America, and north to Alaska (Gompper 2002). Coyote range extension is believed to have been facilitated by 2 synergistic factors. First, human activity and footprint associated with settlement and industry may have opened additional habitat to coyotes (Parker 1995; Gompper 2002). For example, land conversion by forestry and agriculture may have allowed coyotes to expand northward into Québec (Larivière and Crête 1992), and human activity, garbage and animal carcasses associated with the gold rush may have facilitated coyote spread into Alaska (Young and Jackson 1951; Sherman 1981; Thurber et al. 1992). Second, the extirpation of wolves (*C. lupus*) from much of North America may have reduced the competitive pressures limiting coyotes to the Great Plains (Nowak 1978; Thurber and Peterson 1991; Parker 1995; Peterson 1995).

Interference competition in canids is asymmetrical (Peterson 1995; Ballard et al. 2003), a phenomenon that may cause a shift in niche use or competitive exclusion of subordinate species when shared resources are limited (Gause 1934). Negative associations between canid species, such as direct killing of swift foxes (*Vulpes velox*) by coyotes (Kitchen et al. 1999) and coyotes by wolves (Carbyn 1982; Paquet 1991a; Thurber et al. 1992; Arjo and Pletscher 1999), and increased vigilance and decreased rest by coyotes in areas of high wolf use (Switalski 2003), have been documented. However, direct competition for food and interspecific agonistic conflicts do not always result in allopatry

(Paquet 1991b), and in many parts of North America canid species currently coexist (e.g., Carbyn 1982; Schmitz and Lavigne 1987; Thurber et al. 1992; Kitchen et al. 1999). Sympatric distribution in canid species may be facilitated by spatial avoidance, temporal avoidance, or resource partitioning (alternative prey use) (Major and Sherburne 1987; Arjo and Pletscher 1999; Arjo et al. 2002).

Studies have shown that coyotes are often situated outside areas of high wolf use (Berg and Chesness 1978; Fuller and Keith 1981; Dekker 1989; Arjo and Pletscher 1999) or that the 2 species have a low degree of diet overlap (Thurber et al. 1992; Arjo et al. 2002). Because coyotes are opportunistic and generalist predators (Ozoga and Harger 1966; Bowyer et al. 1983), it is often implied that this represents avoidance of wolves by coyotes (Berg and Chesness 1978; Carbyn 1982) rather than differences in habitat selection and prey use (Todd et al. 1985). In contrast, other studies, have shown that coyote home ranges can occur within (or overlap substantively) wolf pack territories (Paquet 1989; Thurber et al. 1992), that activity of the 2 species is frequently synchronous (Paquet 1991a), and that the 2 species have a high degree of dietary overlap (Meleshko 1986). It has been argued that high spatial and dietary overlap may occur where coyotes acquire most of their food by scavenging abandoned wolf-killed prey, particularly ungulates (Paquet 1991b; Arjo et al. 2002).

Coyotes were historically absent from non-prairie Alberta; however, they have expanded north and west to include most of the mountainous and northern boreal forest of the province (Bowen 1981; Fuller and Keith 1981; Gompper 2002). Although these regions roughly delineate wolf distribution in Alberta (Hayes and Gunson 1995), few studies have assessed the interspecific interactions between wolves and coyotes in Alberta. Fuller and Keith (1981) provided information on the location of 1 coyote home range and the capture sites of 4 others, relative to the locations of wolf pack territories in northeastern Alberta. These authors found minimal spatial overlap between coyote home ranges and wolf territories (also see Dekker 1989). Northeastern Alberta is an area of conservation concern for boreal-ecotype woodland caribou (*Rangifer tarandus caribou*) (Dzus 2001; McLoughlin et al. 2003). While wolves have been shown to be the primary predators of caribou in this region (Fuller and Keith 1980; James et al. 2004; Latham et al. 2011b), coyotes are also known predators of caribou in North America, particularly calves (Crête et al. 1990; Crête and Desrosiers 1995). However, with the exception of Fuller and Keith's (1981) note nothing is known about coyote expansion into northeastern Alberta, despite the potentially important implications for caribou conservation and management.

The aim of this study was to expand on Fuller and Keith's (1981) note on coyote-wolf interactions in the boreal forest of northeastern Alberta, and to assess what role recent industrial (forestry and oil and gas) development in the area (Schneider 2002) may have played in facilitating coyote expansion into woodland caribou ranges. We examined 4 interrelated objectives that pertain to coyote range extension into caribou range and coyote interactions with wolves and caribou.

1. Coyote habitat selection: what habitats do coyotes select in caribou range and is there evidence that human footprint has facilitated coyote range extension into northeastern Alberta?
2. Coyote food habits: what prey species do coyotes utilize in caribou range and is there evidence of resource partitioning between coyotes and wolves?

3. Coyote-wolf interspecific interactions: do coyotes show spatial or temporal avoidance of areas used by wolves?

4. Coyote and wolf habitat selection during the caribou calving season: what habitats do coyotes and wolves select compared to caribou during the calving season and is there evidence that spatial overlap between canids and caribou increases at this time of year?

We summarize our results following 2 general themes. First, we discuss those factors that have facilitated coyote range extension into caribou range in northeastern Alberta, with particular emphasis on industrial footprint and coyote interactions with wolves. Second, we discuss the spatial relationships of caribou with historic (wolves) and novel (coyotes) canid predators, as well as the potential implications for caribou population dynamics.

Materials and Methods

STUDY SITE

Our study area was located in the West Side of the Athabasca River (WSAR) and Algar portion of the East Side of the Athabasca River (ESAR) caribou ranges in northeastern Alberta (Fig. 1). This area encompassed approximately 21,000 km^2 of western boreal plains near the town of Wabasca-Desmarais (Lat. 55°57’ N, Long. 113°49 W). Topographic relief is minimal within the 2 caribou ranges (elevation varies from 500 m to 700 m above sea level). The Pelican Mountains located in the adjacent upland mixed-woods in the southwest are the highest point in the study area at approximately 950 m above sea level. The Athabasca River, which flows south to north between WSAR and ESAR, is the lowest point at approximately 400 m above sea level. Numerous other smaller rivers and streams occur throughout the remainder of the study area.

The study area was a naturally fragmented mosaic of peatlands (approx. 60% of the study area) and upland mixed-woods (Latham 2009). Peatlands consisted of black spruce (*Picea mariana*) bogs (approx. 60% of peatlands) and black spruce-tamarack (*Larix laricina*) fens (approx. 30% of peatlands), interspersed by numerous marshes and swamps. Ground cover consisted mainly of Labrador tea (*Ledum groenlandicum*), bog birch (*Betula glandulosa*), sedges (*Carex* spp.), peat moss (*Sphagnum* spp.), and a variety of lichens (e.g., *Cladina* spp. and *Peltigera* spp.). Willows (*Salix* spp.) were abundant along watercourses. During the snow-free period, peatlands were typified by shallow surface water: the water level in bogs was typically 40–60 cm below the surface, whereas in fens it was at or near the surface (Vitt 1994). Upland mixed-woods consisted primarily of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*) (see Bradshaw et al. (1995) and Latham (2009) for a detailed description of vegetation in the study area).

Our study area was located on the southwest corner of the Athabasca oil-sands deposits (Crandall and Prime 1998). Exploration for and extraction of oil and gas by the energy sector increased markedly in the study area in the mid- to late-1990s (Crandall and Prime 1998; Schneider 2002). For example, Tracz (2005) reported that gas, oil, and heavy oil well placement in our study area increased cumulatively by approximately 70% since 1995; a percentage that is considered to be representative of changes in the footprint associated with the energy sector. Similarly, the footprint associated with forestry increased during this time period; however, because of the scarcity of merchantable timber in peatlands, logging was primarily confined to upland forests adjacent to the caribou ranges (Schneider 2002). Associated with these industrial practices was an average of 1.8 km/km^2 of all-season roads, seasonal roads, winter access-ways, trails, pipeline right-of-ways, transmission lines, conventional seismic lines, and 2–3-m-wide low impact seismic. Conventional seismic were the most ubiquitous industrial linear feature in the region, and were widespread in peatlands and uplands (Schneider 2002).

The main prey species available to coyotes and wolves during our study were moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), woodland caribou, beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), snowshoe hare (*Lepus americanus*), and mice and voles (*Peromyscus* spp., *Clethrionomys* spp., and *Microtus* spp). In addition, elk (*Cervus elaphus*) and mule deer (*O. hemionus*) occurred at low densities in some parts of the study area (Latham 2009). Black bears (*Ursus americanus*), Canada lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*) were also present. Trapping of fur-bearing mammals has occurred in the study area since the early-1900s (Stelfox and Wynes 1999; Wetherell and Kmet 2000).

ANIMAL CAPTURE AND RADIO-COLLARING

Nine coyotes and 32 wolves were caught between January 2006 and March 2007. Coyotes and wolves were trapped in summer using modified foot-hold traps and caught in winter via helicopter net-gunning (University of Alberta Animal Care Protocol No. 471503 and Alberta Research and Collection Permit Nos. 23428 and 23669). Captured animals were fitted with a very high frequency (VHF; coyotes: *n* = 2; wolves: *n* = 20) or a global positioning system (coyotes: GPS 3300, *n* = 6, GPS 4400S, *n* = 1; wolves: GPS 4400S, *n* = 12) radiocollar (Lotek Wireless, Aurora, Ontario, Canada). Coyote GPS radiocollars were programmed with a 30-minute relocation schedule from late-April to mid-June in 2006 and with a 4-hour relocation schedule for the remainder of the study (2006 to early-2008). Wolf GPS radiocollars were programmed with a 45-minute relocation schedule from late-April to mid-June (i.e., the wolf denning season) in 2006 and with a 2-hour relocation schedule for the remainder of the study (2006 to early-2008). Radiocollars were monitored fortnightly by fixed-wing aircraft.

During the monitoring period individual coyotes wore active VHF or GPS collars for 51–286 consecutive days (mean = 200, SD = 110), resulting in 23–2,946 telemetry points per individual (mean = 1,408, SD = 1,332). Wolves wore active GPS collars for 30–265 consecutive days (mean = 170, SD = 87), resulting in 296–2,562 locations per individual (mean = 1,651, SD = 707). Previous trials in Alberta using Lotek GPS collars (with a high number of channels) have demonstrated minimal GPS bias, suggesting that corrections were unnecessary (Hebblewhite et al. 2007). We defined seasons as snow (Oct. to Mar.) and snow-free (Apr. to Sep.) based on seasonal differences in wolf pack cohesion (Fuller 1989; Latham 2009) and strong seasonal caribou mortality bias (McLoughlin et al. 2003).

Telemetry data of caribou were obtained from 42 VHF radio-collared (Lotek Wireless, Aurora, Ontario, Canada) adult female caribou in the WSAR range collected between 2003 and 2008. Caribou were captured in winter using a helicopter and net-gun (McLoughlin et al. 2003). Caribou were relocated every 3 to 7 days during the calving season, yielding 296 locations within our study area.

LANDSCAPE COVARIATES

Explanatory variables included in our analyses were derived from a Geographic Information Systems (GIS) of the study area using ArcGIS 9.3 (ESRI 2008) and included: distance to- covariates, linear feature density, land cover-type, and relative probability of wolf occurrence. Distance to- covariates were calculated as the straight line distance (km) to the nearest human settlement (i.e., towns and hamlets), all-season road, pipeline, seismic line, oil and gas well, minor rivers and streams, and upland habitat edge (Table 1). We defined all-season roads as paved and maintained gravel roads open to year-round vehicle use. Linear feature density included all anthropogenic linear features (i.e., seismic lines, roads, pipeline-right-of-ways, power lines, and winter access-ways), and was calculated as edge density (length/area) within a 500 m buffer around each coyote, wolf, or caribou location.

We obtained land cover-type from digital forest inventory data (Alberta Vegetation Inventory (AVI); Nesby 1997) classified into: bog, deciduous, fen, mixed-wood, upland conifer, water, recent burns, anthropogenic (excluding forestry cutblocks and towns), young cutblocks (<6-yr old), middle-aged cutblocks (6–30-yr old), and old cutblocks (>30-yr old). We converted land cover-types to a 25 m × 25 m pixel raster map. We used the Alberta Ground Cover Classification (AGCC; Young et al. 2006) to obtain land cover-types for 3 portions of the study area where the AVI was unavailable. We included land cover-types in analyses as the proportion of each type within a 500 m buffer around each coyote, wolf, or caribou location.

The relative probability of wolf occurrence was modeled as a resource selection function (RSF; Manly et al. 2002). Using mixed-effects logistic regression we developed seasonal wolf RSFs based on 5,244 snow locations and 9,174 snow-free locations and an equivalent number of random locations drawn within the study area. A random intercept for each of 8 wolf packs was included to control for group-level heterogeneity in resource selection. The relative probability of wolf occurrence was modeled as a function of the landscape covariates described in the previous paragraphs (see Latham 2009 for detailed methodology).

STATISTICAL ANALYSIS

Coyote habitat selection

To assess what industrial and natural landscape features were allowing coyote expansion into caribou range we used a used-available RSF design comparing industrial and natural feature covariates at coyote GPS locations (used) and random (available) locations using logistic regression (Johnson et al. 2006; Boyce et al. 2002). As suggested by Hebblewhite and Merrill (2008), we incorporated mixed-effects into RSF models by using generalized linear mixed models (GLMM) to control for group-level heterogeneity in resource selection by including a random intercept for each coyote. Because we were interested in coyote habitat selection within a caribou range (i.e. second order selection, Johnson 1980; also see Boyce 2006) we used the union of home ranges among coyotes (defined as the 100% minimum convex polygon (MCP) encompassing all of the coyote locations) to represent available habitat to coyotes and sampled randomly from within this polygon using a 1:1 ratio of used to available points. This equated to 0.5 and 1 random points/km^2 of coyote territory during the snow and snow-free season, respectively. Separate models were fitted to assess resource selection during snow and snow-free months.

The main motivation for this analysis was to assess the effects of natural and anthropogenic features on coyote habitat selection. Accordingly, we only fitted a global model including all of the covariates of interest and inferred their positive, negative or null influence on coyote seasonal habitat selection, rather than comparing multiple alternative models. We screened against including collinear variables using a $|r| = 0.7$ as a threshold cut-off value (Tabachnick and Fidell 1996; Hosmer and Lemeshow 2000). We verified the assumption of linearity between the relative selection of the response and each candidate covariate using smoothed scatterplots (Hosmer and Lemeshow 2000); if non-linearities were detected, appropriate transformations were included for the corresponding covariate terms. We used k-fold cross-validation to evaluate model performance (Boyce et al. 2002).

Coyote food habits

To assess prey species composition in coyote diet, we collected scats at areas of recent coyote activity (e.g., den, kill, and resting sites) that were identified from telemetry locations between January 2006 and January 2008. Targeting known areas of coyote use also reduced the likelihood of confusing coyote scats with those of sympatric canid species (wolves and red foxes). However, if the scat had no tracks associated with it to verify it as coyote, it was not found near a coyote den, or it was >25 mm in diameter (Reed et al. 2004) we excluded it from the analysis. We randomly selected 20 hairs per scat sample for species identification, and converted them to percentages of prey species in coyote diet. Hair and other contents (bones and feathers) of scats were identified to species following Adorjan and Kolenosky (1969) and Kennedy and Carbyn (1981). In addition, we created a reference set based on prey hair samples. The reference set was used to aid species identification, and to evaluate observer reliability. Finally, percent occurrence of each prey species in coyote diet was compared to those obtained in wolf diet by Latham (2009) using a similar methodology.

Coyote-wolf interspecific interactions

To study spatial and temporal relationships between coyotes and wolves, and to assess whether coyotes use industrial footprint as a spatial refuge from wolves, we used 3 approaches: first we assessed coarse spatial overlap between coyote and wolf home ranges; second we assessed coyote selection for natural and anthropogenic landscape features relative to wolves; and third we assessed whether relative habitat selection by coyotes as compared to wolves changed between day and night.

To assess coarse spatial overlap between coyotes and wolves, we created seasonal kernel density estimators (KDE) for both species using least squares cross validation to estimate the smoothing factor, h, and an isopleth of 90% to define coyote or wolf territory boundaries (Börger et al. 2006). We used telemetry locations from 1 VHF- and 5 GPS-collared coyotes (one of which was assessed separately in 2006 and 2007), and 11 GPS-collared wolves belonging to 8 packs to calculate KDEs using Home Range Tools for ArcGIS (Rodgers et al. 2007) and Hawth's Analysis Tools (Beyer 2004). The number of locations used to define territories ranged from 23 to 2,945 for coyotes, and from 772 to 3,799 for wolf packs.

To assess fine scale spatial relationships between coyotes and wolves, we randomly selected 1 daily location per coyote and wolf, yielding 415 and 561 coyote locations and 618 and 1,099 wolf locations during the snow and snow-free seasons, respectively. We then used logistic regression to estimate coefficients for latent selection difference (LSD) functions

(Czetwertynski 2007; Latham et al. 2011a) to contrast the differences in habitat selection between coyotes and wolves. This method allows for direct comparisons of habitat selection between two groups of interest and produces quantifiable measurements of strength of relationships (Czetwertynski 2007). A key assumption of this method is that all habitat types should be equally available to both species within the study area; locations of coyotes and wolves in Fig. 1 show that this assumption was not violated in our study area. This model does not work with individuals as random factors and consequently does not correct for an unbalanced sampling design. We estimated standard errors (SE) using the Huber-White sandwich estimator (White 1980) grouping data by individual coyote or wolf, i.e., we assumed that observations were independent across clusters (between coyotes or wolves) but not within clusters (data points associated with a given coyote or wolf). We used LSDs to assess spatial separation between coyotes and wolves by evaluating the relative difference in selection for each of the variables described in Table 1. The methods for interpreting the coefficients follow Latham et al. (2011a).

We further assessed temporal separation of coyotes from wolves using LSD functions. We partitioned coyote and wolf GPS locations into day and night, and compared day and night locations with respect to the variables listed in Table 1. We designated locations as day or night based on averaged monthly sunrise and sunset tables for the study area (http://www.hia-iha.nrc-cnrc.gc.ca/). This analysis was done separately for the snow and snow-free seasons.

Coyote and wolf habitat selection during the caribou calving season

We assessed patterns of habitat selection by coyotes and wolves at the population level during the caribou calving season (15 Apr. to 30 Jun.) using telemetry locations from 3 coyotes (one of which was assessed separately in 2006 and 2007) and 8 wolf packs. We estimated RSFs using mixed-effects logistic regression (Johnson et al. 2006), including a random intercept for each coyote or wolf pack (Skrondal and Rabe-Hesketh 2004; Gillies et al. 2006; Hebblewhite and Merrill 2008). To avoid including areas for which we did not have information for coyotes or wolves, we constrained the domain of availability to the 100% MCP encompassing all of the coyote or wolf pack locations (i.e., second-order selection, Johnson 1980; also see Boyce 2006), and drew random locations from this area using a 1:1 ratio of used to available locations (which equated to approximately 2 and 0.6 random points/km^2 of coyote and wolf territory, respectively). For this analysis, we only fitted a global model including all of the covariates of interest, and from there inferred their positive, negative or null influence on coyote or wolf habitat selection during the caribou calving season. We verified the assumption of linearity between the relative selection of the response and each candidate covariate using smoothed scatterplots (Hosmer and Lemeshow 2000). We used k-fold cross-validation to evaluate model performance (Boyce et al. 2002).

We further assessed calving-season habitat selection for coyotes and wolves individually. We limited this analysis to testing the hypothesis that coyotes and wolves select areas with a high proportion of bogs and (or) fens and areas farther from upland habitat edges, i.e., those habitat types that are known to be selected by caribou. We used the same telemetry locations that were used for the population-level analysis; these were then compared with random locations, generated using a 1:1 ratio, to estimate a used-available

RSF (Johnson et al. 2006). Random locations were drawn from within the 100% MCP encompassing all of the locations collected for that coyote or wolf pack. The same covariates (Bog + Fen + Dupl) were fitted to a model for 3 individual coyotes (one of which was assessed separately in 2006 and 2007) and 8 individual wolf packs. The sign, magnitude, and significance (i.e., confidence intervals not spanning 0) of the coefficients for each of the variables within the model were assessed as evidence for or against the hypothesis that coyotes and wolves were selecting habitats preferred by caribou.

Finally, to assess spatial overlap between coyotes and caribou and wolves and caribou, we randomly selected 1 daily location per coyote or wolf pack during the calving season, yielding 233 coyote and 586 wolf locations. We chose to include a slightly larger sample interval for the caribou data (i.e., 2003–2008, as opposed to 2006–2008 for canids) to increase the sample size to 296 caribou locations within the study area and sample interval. We used LSD functions to contrast the differences in habitat selection between caribou and coyotes and caribou and wolves during the calving season. We estimated standard errors (SE) using the Huber–White sandwich estimator (White 1980) grouping data by individual coyote, wolf pack or caribou.

All statistical analyses were performed in R version 2.10.1 for Windows (R Development Core Team 2009).

Results

Between 2006 and 2008, we radiocollared 9 coyotes within the WSAR and Algar portion of ESAR caribou ranges. Three of the coyotes were transients and dispersed out of the study area shortly after being collared. The longest recorded dispersal was approximately 164 km straight line distance from the west of the study area to the town of Fort McMurray (Lat. 56°44’ N, Long. 1131°24 W). The remaining 6 coyotes provided 8,490 locations (range: 23–2,946). Coyote 5 showed a complete territory shift between 2006 and 2007, thus we treated its corresponding annual telemetry points separately in all analyses.

Coyote habitat selection

During the snow season, habitat selection by coyotes was positively influenced by the proportion of anthropogenic habitat, bog, deciduous forest, and young and middle-aged cutblocks (<30 years old), as well as distance to human settlements, rivers and streams, pipelines and seismic lines (Table 2). Habitat selection was Gaussian relative to the distance to all-season roads, indicating that coyotes preferred areas closer to these features. Coyote selection for wells was also Gaussian and indicated that the relative probability of selection was highest close and at intermediate distances to these features and decreased rapidly as distance from these features increased. The relative probability of coyote selection was high in areas of high wolf use. The k-fold cross-validation showed that the RSF model for coyotes during the snow season performed well. The mean Spearman’s rank correlation coefficient from 5-fold cross-validation was 0.6606 ($P < 0.05$).

During the snow-free season, habitat selection by coyotes was positively influenced by distance to all-season roads, rivers and streams, upland boundaries, and pipelines, but was negatively influenced by the proportion of bog, mixed-wood forest, and middle-aged cutblocks (Table 2). The relative probability of coyote selection was marginally significant in areas of high wolf use. The k-fold cross-validation showed that the RSF model for coyotes in the snow-free season performed well. The mean Spearman’s rank correlation coefficient from 5-fold cross-validation was 0.9879 ($P < 0.05$), indicating that the model correctly predicted habitat use by coyotes.

Coyote food habits

The most common prey species in coyote scats were mouse/vole (*Peromyscus* spp., *Clethrionomys* spp., and *Microtus* spp; 44%) and muskrat (*Ondatra zibethicus*; 40%) (Fig. 2). Deer (29%) were also common and included an equal proportion of adult and fawn deer. Beaver, grouse (*Bonasa umbellus* and *Falcipennis canadensis*), red squirrels (*Tamiasciurus hudsonicus*), insects, and vegetation were uncommon (approx. 4%) in scats. Caribou calf, snowshoe hare, and woodchuck (*Marmota monax*) were rare (<2%).

When compared to wolf diet, both species showed a relatively high use of deer (Fig. 3). Beaver and moose were common in wolf diet, whereas they were relatively uncommon or, in the case of moose, completely absent in coyote diet. Caribou was rare in both wolf and coyote diet. Small prey species were the most common food items in coyote diet, whereas small prey species occurred in only 11.3% of wolf scats (Fig. 3). Small prey in wolf scats included: grouse, mouse and vole, muskrat, red squirrel, snowshoe hare, and woodchuck.

Coyote-wolf interspecific interactions

Coarse-scale assessment of spatial overlap indicated that home ranges of 5 coyotes overlapped with wolf pack territories during the snow season (mean areal overlap = 49.1%, range = 2.7% to 81.8%), whereas only 2 coyote home ranges overlapped wolf pack territories in the snow-free season (areal overlap was <2% in both cases).

During the snow season, coyotes selected areas with a high proportion of anthropogenic habitat, bog, deciduous and upland conifer stands, and lakes relative to wolves (Table 3). Coyotes also selected for areas closer to all-season roads and seismic lines relative to wolves. During the snow-free season, coyotes selected for areas with a high proportion of deciduous forest, low proportion of middle-aged cutblocks, and closer to all-season roads relative to wolves.

Temporal analyses indicated that during the day in the snow season, coyotes selected for anthropogenic habitats, deciduous and upland conifer stands, and lakes relative to wolves (Table 4). Further, coyotes used areas closer to all-season roads and seismic lines but further away from upland boundaries compared to wolves. During the day in the snow-free season, coyotes selected areas with a high proportion of deciduous and upland conifer stands, fen, lakes, a high density of linear features, and close to all-season roads relative to wolves (Table 4).

During the night in the snow-season, coyote habitat selection was positively influenced by the proportion of anthropogenic habitat, deciduous stands, fen, and lakes relative to wolves (Table 5). Coyotes also selected for areas closer to seismic lines but further away from upland boundaries compared to wolves. During the night in the snow-free season, coyote habitat selection was positively influenced by the proportion of deciduous and upland forest stands, fen, and lakes relative to wolves. Coyotes also selected for areas closer to all-season roads and upland boundaries relative to wolves (Table 5).

Coyote and wolf habitat selection during the caribou calving season

During the caribou calving season, coyote habitat selection was positively influenced by the proportion of bog, deciduous, mixed-woods, upland forested stands, and lakes (Table 6). Habitat selection was Gaussian relative to the proportion of fen, indicating that coyotes preferred areas with intermediate levels of this type of vegetation. Coyotes also selected for areas closer to all-season roads, rivers and streams, pipelines, and human settlements during the caribou calving season. The 5-fold cross-validation showed that the RSF for coyotes during the caribou calving season performed well. The mean Spearman's rank correlation coefficient from 5-fold cross-validation was 0.7939 ($P < 0.05$), indicating that the model correctly predicted habitat use by coyotes.

At the individual level, 2 coyotes selected black spruce bogs and 2 coyotes avoided black spruce bogs (Table 7). Three coyotes selected tamarack-dominated fens, whereas 1 coyote showed neither avoidance nor selection. The relative probability of use decreased significantly with increasing distances from an upland boundary for 1 coyote, as evidenced by the negative coefficient for this variable. This indicates that although coyote 5 showed selection for fens during 2006, this may have been confined to peripheral rather than core fen habitat. However, the opposite pattern was observed for coyote 9, suggesting that this coyote foraged in fens farther from uplands and into core caribou habitat. The remaining 2 coyotes showed neither selection nor avoidance of upland boundaries.

During the caribou calving season, habitat selection by coyotes relative to caribou was positively influenced by the proportion of deciduous and upland conifer stands (Table 8). Conversely, coyotes avoided areas with a high proportion of fen relative to caribou. Coyotes also selected for areas closer to all-season roads and upland habitat edges compared to caribou (Table 8).

During the caribou calving season, wolf selection for deciduous and upland conifer forests was Gaussian, indicating that wolves preferred areas with intermediate levels of these types of vegetation (Table 9). Wolves selected for areas closer to rivers and streams, upland boundaries, and seismic lines during the caribou calving season. Wolves selected areas at intermediate distances from all-season roads and human settlements. The k-fold cross-validation showed that the RSF for wolves during the caribou calving season performed well. The mean Spearman's rank correlation coefficient from 5-fold cross-validation was 0.8182 ($P < 0.05$), indicating that the model correctly predicted habitat use by wolves.

At the individual level, 7 wolf packs showed avoidance of bogs of black spruce, and 1 pack showed neither avoidance nor selection (Table 10). Alternatively, 2 wolf packs showed selection for tamarack-dominated fens, 2 packs showed avoidance, and 4 packs showed neither avoidance nor selection. The relative probability of use significantly decreased with increasing distances from an upland boundary for 4 wolf packs, as evidenced by the negative coefficient for this variable. However, the opposite pattern was observed for the Rock Island pack and possibly the Calling pack, suggesting that some packs foraged farther from uplands and into core caribou habitat.

During the calving season, wolf habitat selection relative to caribou was positively influenced by the proportion of deciduous and upland conifer stands (Table 11). Conversely, wolves avoided areas with a high proportion of bog and fen relative to caribou. Wolves also selected areas closer to streams and oil and gas wells but further away from all-season roads and pipelines compared to caribou (Table 11). Finally, wolves selected areas with a high density of linear features compared to caribou.

Discussion

Coyote range expansion and interspecific interactions with wolves

Coyote range expansion in North America generally has been associated with decreased interference competition with wolves (Peterson 1995; Gompper 2002) and increased human activity and footprint (Parker 1995; Gompper 2002). We found that coyote expansion into WSAR and ESAR caribou ranges was associated with several types of human disturbances. In particular, we found a positive year-round association with all-season roads and pipelines, as well as selection for areas closer to human settlements, oil and gas wells, seismic lines, and young to middle-aged cutblocks during the snow season. Fuller and Keith (1981) trapped coyotes near garbage dumps or human settlements in the Oil Sands Area of northeastern Alberta in the 1970s, suggesting that coyote range extension into the Fort McMurray area may similarly have been facilitated by anthropogenic factors. Human settlement and industrial activity and footprint can provide novel food sources (e.g. garbage) and a spatial refuge from the competitive pressures of coexisting with wolves. Interestingly, our results also showed that coyotes selected areas of high wolf use, especially during the snow season, suggesting that wolves are either not a threat to coyotes in this region or that coyotes accrue some benefit from selecting areas of high wolf use. Although wolves can kill coyotes (Berger and Gese 2007), they also provide significant food subsidies in the form of scavenging opportunities (Paquet 1991a; Wilmers et al. 2003; Atwood and Gese 2008; Merkle et al. 2009). Strong selection of areas of high wolf use by coyotes in winter months might result if coyotes scavenge wolf-killed ungulates at this time of year when more common prey items (e.g., mice, voles, and muskrats) are not as available (or as easy to hunt) because of snow and frozen rivers and streams.

Sympatric distribution of canid species is facilitated by spatial avoidance, temporal avoidance, or resource partitioning. We found that small prey species were the most common items in coyote diet, with mouse, vole or muskrat present in approximately 80% of coyote scats. When compared to wolves, resource partitioning between the 2 species was apparent, with <10% of wolf scats containing small prey species. However, white-tailed deer were important prey for coyotes (approx. 30% occurrence) and wolves (approx. 40% occurrence). White-tailed deer have recently invaded WSAR and ESAR and represent approximately 30 to 40% of prey biomass in the environment and contribute an estimated 30 to 40% of prey biomass to wolf diet (Latham et al. 2011b). Our results also show that deer are important prey for coyotes and have potentially aided coyote expansion into caribou range in northeastern Alberta. Thus although resource partitioning was evident, coyote and wolf diet overlapped substantively with regard to deer. While coyotes were observed hunting deer (A. D. M. Latham, personal observation), the high percentage of deer in coyote diet also might have resulted from coyotes scavenging wolf kills, although if this were the case we would have expected to find a higher percentage of moose and beaver in coyote scats. Alternatively, coyotes might have scavenged road-killed deer, possibly explaining (at least partly) coyote selection for all-season roads. In any case, our results support evidence that deer have become a major force of ecological change (Fuller and Gill 2001; Côté et al. 2004), not only supporting a numeric response by wolves (Latham et al. 2011b) but also facilitating the expansion of a novel predator into caribou range.

Despite finding evidence for partitioning of prey species, we found little evidence for spatial separation between coyotes and wolves at a coarse-scale. Our analysis of relative habitat selection by coyotes compared to wolves showed no difference in selection between these 2 canid species for most of the habitat variables analyzed. However, we did find that all-season roads were selected by coyotes but not by wolves and that coyote selection for seismic lines and anthropogenic habitats during the snow season was significantly higher compared to wolves. These results suggest that coyotes may use human-created features to spatially separate from wolves at a fine-scale. This is further supported by Latham et al. (*Accepted*) who showed that wolves avoided seismic lines during winter and all-season roads year-round, suggesting that these features may afford coyotes a refuge from the competitive pressures of coexisting with wolves. Our temporal analyses of space use by coyotes and wolves further supported these results.

Previous studies have shown that coyotes do not show complete spatial separation from wolves but rather modify space use by displaying adaptive resource selection in response to escalating risk of encountering wolves (Atwood and Gese 2010). Our results support these claims, whereby coyotes selected upland forest-types commonly used by wolves, possibly attracted by potential scavenging benefits, but also selected anthropogenic features at a fine-scale, possibly to reduce escalating risk of encountering wolves. Wolf avoidance of human footprint relative to coyotes might result from increased persecution of wolves by humans near these features, whereas the positive effects (food and spatial refuge from wolves) of using these features for coyotes may outweigh the negative effects (persecution by humans).

Interference competition with wolves appears to have resulted in a transient coyote population in our study area. Three of the 9 coyotes that we radiocollared showed no fidelity to a home range during the period of time that we monitored them and all dispersed out of our study area to unknown locations. Further, only 1 non-transient coyote showed home range fidelity for more than 1 year. Because we did not radiocollar coyotes in high-quality upland habitat or near towns, areas where coyotes are known to have occurred for a number of decades (Fuller and Keith 1981), we do not know if the high degree of transiency was confined to caribou range or also occurred outside of this poor quality coyote habitat. Transient coyote dispersal from our study area with non-downloadable GPS collars reduced our sample size ($n = 6$) for habitat selection analyses. However, the high degree of transiency and lack of long-term home range fidelity suggests a mechanism, adaptive space use, by which coyotes are able to extend their range into boreal caribou ranges in northeastern Alberta and to coexist with wolves in this environment. We suggest that shifting patterns of space use and habitat selection by coyotes may have arisen from 3 non-mutually exclusive factors: (1) exploratory forays by coyotes dispersing from agricultural and urban areas to the south and west of the study area that are attempting to find available space to establish a territory; (2) within caribou range, there may be a lack of available space for immigrant coyotes to establish a territory outside areas of high wolf use because of already established coyotes; and (3) shifting spatiotemporal patterns of activity associated with industry (e.g., exploration for oil and gas reserves or logging) and subsequent transiency by coyotes as they follow the food source associated with humans or the fine-scale refugia from wolves provided by human activity.

Coyote and wolf use of caribou range during the calving season

Wolves have been shown to be the primary predators of caribou in northeastern Alberta (Fuller and Keith 1980; James et al. 2004; Latham et al. 2011b); however, coyotes have been shown to predate caribou, particularly calves, elsewhere in North America (Crête et al. 1990; Crête and Desrosiers 1995). To assess the role of coyotes and wolves as predators of caribou calves, we analyzed population-level habitat selection of these 2 predators during the time of the year when calves are most vulnerable to predation. We found that at the population level coyotes selected for bogs and fens during the calving season; however, they also selected upland boundaries, which suggests that use of bog and fens was limited to those patches close to upland habitat types such as deciduous, mixed-wood and upland conifer forests. In addition, coyotes showed strong selection for all-season roads, pipelines, rivers and streams, and human settlements.

A number of recent studies have demonstrated the occurrence of individual specialization within animal populations (e.g., Bolnick et al. 2003; Estes et al. 2003; Urton and Hobson 2005), with important ecological, evolutionary, and conservation implications. Accordingly, we investigated individual coyote selection for caribou preferred habitats, i.e., black spruce bog, black spruce-tamarack fen, and areas further away from upland boundaries (Bradshaw et al. 1995; Stuart-Smith et al. 1997). We found that 2 of 4 coyotes selected bog and 2 of 4 coyotes selected fen irrespective of their distance from an upland boundary. Conversely, Coyote 5 (in 2006) selected fen habitat that tended to be close to an upland boundary. This result suggests that approximately half of the resident population of coyotes in or adjacent to caribou range forage in those habitats selected by caribou during the calving season and represent a potential source of mortality for calves when they are most vulnerable to predation. However, despite finding that at least half of the coyotes selected for caribou-preferred habitat, our assessment of spatial overlap between coyotes and caribou showed that in general coyotes selected for upland habitat types and areas close to anthropogenic features relative to caribou. Interestingly, we found that coyotes and caribou did not differ in their selection for bogs during the calving season; however, coyote selection tended to be restricted to patches of bog habitat close to upland boundaries compared to caribou.

Wolf population-level habitat selection during the caribou calving season was highest in upland forest patches (deciduous and conifer), and close to small rivers and streams and seismic lines. Wolves also showed selection for areas at intermediate distances from all-season roads and human settlements. Previous studies have reported the importance of rivers and streams for wolves in snow-free months, probably because they provide easy travel, and because these are areas where prey live and consequently areas where wolves maximize their hunting effort (Mech and Boitani 2003). Further, Latham et al. (*Accepted*) showed that wolves used seismic lines as movement corridors in the snow-free season and suggested this might result in increased forays into caribou-preferred habitats (bogs and fens) by wolves, thus potentially increasing predation risk for caribou close to these features.

Our individual pack-level analysis of wolf selection for caribou preferred habitats showed that 25% (2 out of 8) of the wolf packs in our study area selected for fen patches irrespective of their distance from an upland habitat boundary. However, our assessment of spatial overlap between wolves and caribou showed that wolves were significantly less likely to be found in bogs and fen, and more likely to be found in deciduous and upland conifer stands than caribou. Our results suggest that woodland caribou in northeastern Alberta attempt to spatially segregate from not only wolves and alternative prey (James et al. 2004), but also from alternative predators such as coyotes and black bears (also see Latham et al. 2011a). However, variation in habitat selection by individual wolf packs, coyotes, and black bears suggests that between 25 and 50% of the predator population selects for caribou-preferred habitats, suggesting that these predators may be contributing to the low survival of adults and calves in this area (Dzus 2001). This is further supported by caribou remains found in coyote (calf remains in 2% of scats) and wolf (adult and possible calf remains in 5% of scats) scats (Latham 2009; also see McLouglin et al. 2003).

Summary

Little is known about the geographic range expansion of coyotes into the boreal forest or their ecology in this region, despite their potential importance as alternative predators of threatened woodland caribou in the region. We extended upon the documentation of coyotes in the Oil Sands Area, north of Fort McMurray, northeastern Alberta, by providing an assessment of coyote habitat selection, diet, and spatiotemporal relationships with caribou, wolves, and industry. We found strong evidence for the hypothesis that industrial footprint has facilitated coyote range expansion into caribou range and may be providing a fine-scale refuge from interference competition from wolves. In general, coyotes and wolves showed resource partitioning, although white-tailed deer was common in the diet of both canid species. We suggest that the expanding distribution of white-tailed deer might be a contributing factor in the northward range extension of coyotes, in addition to causing a positive numeric response by wolves in the region. At the population level, wolves avoided caribou-preferred habitats; however, 2 packs selected fens suggesting that these packs may specialize on prey species (beaver, caribou, and moose) found in this habitat. Conversely, coyote selection for caribou-preferred habitats was evident (albeit based on a small sample size) with all coyotes assessed showing selection for bogs or fens. The transient behaviour of coyotes that were radiocollared, but from which we could not obtain sufficient data to conduct habitat selection analyses, suggests that these individuals may similarly have travelled and hunted in caribou-preferred habitats. However, scat analyses revealed that caribou were rare in coyote diet, a phenomenon also reported for wolves in WSAR (Latham et al. 2011b). Despite this result, predation has been shown to be the main proximate cause of mortality for caribou in northeastern Alberta (Dzus 2001) and even limited predation on adults and calves can have a significant impact on caribou populations. Because of the inherent difficulties of documenting predation on rare species (Latham et al. 2011a), we recommend that management actions to conserve caribou should focus on alternative predators (black bears and coyotes) in addition to wolves.

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