



## Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines

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Population increases of primary prey can negatively impact alternate prey populations via demographic and behavioural responses of a shared predator through apparent competition. Seasonal variation in prey selection patterns by predators also can affect secondary and incidental prey by reducing spatial separation. Global warming and landscape changes in Alberta's bitumen sands have resulted in prey enrichment, which is changing the large mammal predator–prey system and causing declines in woodland caribou *Rangifer tarandus caribou* populations. We assessed seasonal patterns of prey use and spatial selection by wolves *Canis lupus* in two woodland caribou ranges in northeastern Alberta, Canada, that have undergone prey enrichment following recent white-tailed deer *Odocoileus virginianus* invasion. We determined whether risk of predation for caribou (incidental prey) and the proportion of wolf-caused-caribou mortalities varied with season. We found that wolves showed seasonal variation in primary prey use, with deer and beaver *Castor canadensis* being the most common prey items in wolf diet in winter and summer, respectively. These seasonal dietary patterns were reflected in seasonal wolf spatial resource selection and resulted in contrasting spatial relationships between wolves and caribou. During winter, wolf selection for areas used by deer maintained strong spatial separation between wolves and caribou, whereas wolf selection for areas used by beaver in summer increased the overlap with caribou. Changing patterns in wolf resource selection were reflected by caribou mortality patterns, with 76.2% of 42 adult female caribou mortalities occurring in summer. Understanding seasonal patterns of predation following prey enrichment in a multiprey system is essential when assessing the effect of predation on an incidental prey species. Our results support the conclusion that wolves are proximately responsible for woodland caribou population declines throughout much of their range.

Ecological effects of generalist predators in multiprey systems are complex. Shared predation can permit the coexistence of competitively incompatible species (Roughgarden and Feldman 1975, Gleeson and Wilson 1986), mediate habitat partitioning among prey in spatially heterogeneous environments (Holt 1984), or generate indirect interactions that mimic competition among otherwise non-interacting prey, a phenomenon known as apparent competition (Holt 1977, DeCesare et al. 2010). Where spatial partitioning among prey types occurs and a predator targets habitat occupied by primary prey, secondary prey may be encountered only incidentally (Schmidt 2004). However, incidental predation can adversely affect populations of secondary prey, despite only weakly affecting populations of predators or primary prey (Chaneton and Bonsall 2000, DeCesare et al. 2010).

Prey enrichment occurs when populations of native species increase or when an introduced or invading species enters a system (Müller and Godfray 1997, Roemer et al. 2002). Predators generally exhibit a positive numerical

response to prey enrichment, either through population growth (demographic response; Holt et al. 1994), predator aggregation in a particular patch within a heterogeneous environment (behavioural response; Holt and Kotler 1987, Schmitt 1987), or both. An increase in predator numbers in habitat occupied by primary prey can maintain a high spillover of dispersing predators into habitats occupied by secondary or incidental prey, or result in a proportional increase in cross-edge foraging by predators into these habitats (Holt 1984, Müller and Godfray 1997, DeCesare et al. 2010). Consequently, prey enrichment can negatively impact secondary and incidental prey populations via demographic and behavioural responses of a shared predator, through the process of apparent competition. Apparent competition then results in the two prey species experiencing unequal predation by the shared predator, leading to a negative correlation between the abundance of the two prey species as well as between their population growth trajectories (DeCesare et al. 2010). Thus, prey enrichment as described above can trigger apparent competition, which can cause exclusion of

secondary or incidental prey from otherwise suitable habitat (Holt 1977, 1984) and/or an increase in incidental predation on the secondary prey that can ultimately cause population declines (Wittmer et al. 2005).

Populations of caribou and wild reindeer *Rangifer tarandus* have been declining in many areas in North America and Eurasia (Vors and Boyce 2009). Woodland caribou *R. t. caribou* are a threatened boreal forest species that spatially separate from other ungulates to minimize the risk of predation by wolves *Canis lupus*, their primary predator (Bergerud 1974, Seip 1992, James et al. 2004). Across much of the boreal forest of North America, wolves hunted moose *Alces alces*, their historic primary prey, in upland forest, and only incidentally encountered and killed caribou in old growth coniferous forest or peatlands where the densities of other prey were low (Fuller and Keith 1980, Bergerud 1985, James et al. 2004, McLoughlin et al. 2005, Wittmer et al. 2005). Although incidental predation by wolves was responsible for most caribou mortalities (McLoughlin et al. 2003), spatial separation facilitated coexistence of caribou and moose (James et al. 2004). However, changes in the landscape and recent warmer winters have resulted in prey and predator population increases, which is changing the large mammal predator–prey system and is hypothesized to cause declines in woodland caribou populations across their distribution (Boisjoly et al. 2010, Festa-Bianchet et al. 2011, Latham et al. 2011a, Pinard et al. 2012).

Forest harvesting and energy development activities have converted large tracts of forest within or adjacent to caribou ranges to early-seral-stage forest that is attractive to moose, elk *Cervus elaphus*, and deer *Odocoileus* spp. (Cumming 1992, Serrouya et al. 2011). Recent warmer winters are also believed to have contributed to the range extension and increasing populations of white-tailed deer *Odocoileus virginianus* (hereafter referred to as deer) in the boreal forest across Canada (Côte et al. 2004, Dawe 2011). In northeastern Alberta, Canada, deer have increased 17.5-fold since the mid-1990s and deer have replaced moose as the primary prey of wolves (Latham et al. 2011a). Wolves have shown a strong demographic numerical response to prey enrichment, and their density has nearly doubled since the mid-1970s to approximately 11/1000 km<sup>2</sup> (Fuller and Keith 1980, Latham et al. 2011a). Recent evidence shows that caribou have increased 10-fold in annual wolf diet since the mid-1990s and following deer invasion (James et al. 2004, Latham et al. 2011a).

Although evidence of a demographic response by wolves to prey enrichment is clear (Latham et al. 2011a), potential behavioural responses are less well understood. Spatial overlap between wolves and caribou has increased in tandem with greater deer and beaver *Castor canadensis* in wolf diet (Latham et al. 2011a), but the mechanisms driving increased wolf use of caribou habitat are poorly understood. Season, in particular, may play an important role because most adult woodland caribou mortalities due to wolf predation in western Canada have been shown to occur in summer and early-autumn (i.e. April–October; McLoughlin et al. 2003: 78.8%, n = 112; Whittington et al. 2011: 83.3%, n = 12), and in Finland virtually no wild reindeer were killed by wolves in mid-winter (Kojola et al. 2004). The importance of seasonal variation in predation patterns for

understanding large mammal predator–prey dynamics has recently been highlighted (Sand et al. 2008, Knopff et al. 2010, Metz et al. 2012), and season may also play an important role in apparent competition and incidental predation if it affects the spatial relationships between a generalist predator and its prey (Holt and Kotler 1987, Schmitt 1987, Latham et al. 2011b). Consequently, understanding the relationships between wolves, common prey species (moose, deer, and beaver), and caribou following prey enrichment in both winter and summer is essential for effective management of this system (Boutin et al. 2012, Wittmer et al. 2013).

The objectives of this study were to assess seasonal patterns of prey use and spatial selection by wolves in two woodland caribou ranges in northeastern Alberta that have undergone prey enrichment following recent deer invasion (Latham et al. 2011a), and to determine whether seasonal variation results in changes in predation risk for caribou and in the proportion of wolf-caused adult caribou mortalities in each season. We used a multi-model approach to test three competing hypotheses (historic primary prey, common alternative prey, and total prey biomass). First, we hypothesized that irrespective of season wolves select areas preferred by their historic primary prey, moose, resulting in low spatial overlap between wolves and caribou, and minimal caribou in wolf diet (as found by James et al. 2004). We define moose as the historic primary prey based on studies by Fuller and Keith (1980) and James et al. (2004), and traditional environmental knowledge from Schramm (2005). Our second hypothesis is that wolves select areas preferred by the two most common alternative prey species, deer and beaver. Irrespective of season deer were most abundant in upland forest (Latham et al. 2011a), whereas caribou were more abundant in peatlands, and thus we predict that if wolves select deer, spatial overlap between wolves and caribou will be low in both seasons. Beaver were abundant in uplands and peatlands (Latham 2009), but were largely unavailable in winter (Mech 1966). Thus, if wolves switch to beaver when they become available, we predict higher spatial overlap between wolves and caribou, more caribou in wolf diet, and greater wolf-caused caribou mortalities during summer. The third hypothesis we test is that wolves select areas with the highest total prey biomass, irrespective of season. Because prey biomass was highest in upland forest, we predict that wolf selection for total prey biomass will result in low spatial overlap between wolves and caribou, and minimal caribou in wolf diet at all times of year.

## Methods

### Study site

The study area included 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, Canada (Fig. 1). This area encompassed 21 000 km<sup>2</sup> of western boreal plains near the town of Wabasca-Desmarais (55°57'N, 113°49'W). Topographic relief was minimal within the two caribou ranges (elevation varied

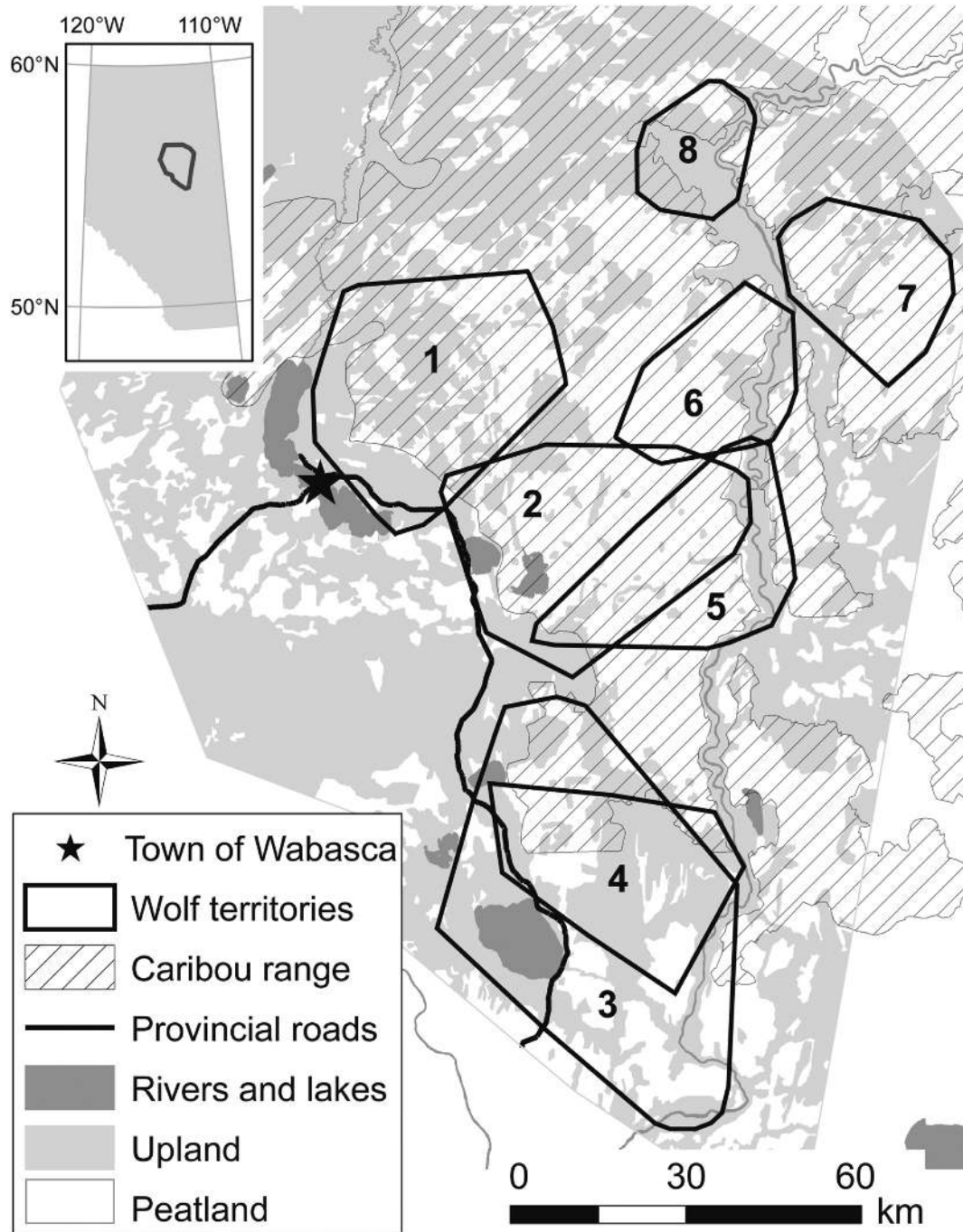


Figure 1. West Side of the Athabasca River and western portion of the East Side of the Athabasca River caribou ranges in northeastern Alberta, Canada (the town of Wabasca is located at 55°57'N, 113°49'W). Solid-line, numbered polygons represent wolf pack territories (100% minimum convex polygons) generated from Global Positioning System data collected between 2006 and 2008. Pack names are: (1) GoCan, (2) Pelican Lake, (3) Rock Island, (4) Calling, (5) Pelican River, (6) Joli, (7) Algar, and (8) Livock. Rock Island and Calling occupied the same southern area, but in different years.

from 500 to 700 m). Vegetation consisted of a naturally fragmented mosaic of peatlands (approximately 60% of the study area) and upland mixed-woods (Fig. 1). Peatlands consisted of black spruce *Picea mariana* bogs (approximately 60%) and black spruce-tamarack *Larix laricina* fens (approximately 30%), interspersed by numerous marshes and swamps. Willows (*Salix* spp.) were abundant along water-courses. During summer, peatlands were typified by shallow

surface water (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 Latham et al. 2011a for further details on topography and vegetation).

Potential prey for wolves included moose, woodland caribou, deer, beaver, and snowshoe hare *Lepus americanus*. Moose were most abundant in uplands during winter



(James et al. 2004), and in uplands and near riparian features and wet meadows during spring and summer (Osko et al. 2004, Latham 2009); woodland caribou were found almost exclusively in peatlands (Stuart-Smith et al. 1997); deer were abundant in uplands year-round; and beaver were abundant around lakes, rivers, and streams in both peatlands and uplands (Latham 2009). Elk *Cervus elaphus* and mule deer *O. hemionus* occurred at low densities within small portions of the study area. Black bears *Ursus americanus*, Canada lynx *Lynx canadensis*, red fox *Vulpes vulpes*, and coyote *Canis latrans* also occurred in the area. Wolves have been trapped at low levels in the study area since the early-1900s (James et al. 2004); no other type of intensive wolf management has occurred in the area.

Estimates of moose densities vary spatially across northeastern Alberta (range: 13–35/100 km<sup>2</sup>; Alberta Environmental Protection 1998, 2003). However, Latham et al. (2011a) found little temporal variation in the number of moose seen in aerial surveys conducted in our study area between 2005 and 2007 (range from all surveys = 3.0–4.8 moose seen 100 km<sup>-1</sup> of aerial flight path). Provincial deer density estimates for the boreal-agricultural fringe directly to the south of the study area were 164/100 km<sup>2</sup> (± 23.8%) in 2002 and 174/100 km<sup>2</sup> (± 19.1%) in 2003; whereas Latham (2009) reported a lower estimate of 76.5/100 km<sup>2</sup> for the study area in 2005–2007 based on a ratio-estimator. Further, Latham et al. (2011a) showed an increasing trend in the number of deer seen during aerial surveys between 2005 and 2007 (1.8 ± 0.8 (mean ± SE) and 5.2 ± 0.8 deer seen 100 km<sup>-1</sup> of aerial flight path, respectively). Caribou density estimates for our study area range between 4.1 and 7.7/100 km<sup>2</sup> (Stuart-Smith et al. 1997), and Latham (2009) found little temporal variation in number of caribou seen in aerial surveys conducted between 2005 and 2007 (range from all surveys = 0.9–2.3 caribou seen 100 km<sup>-1</sup> of aerial flight path). Beaver density in our study area was estimated at 154/100 km<sup>2</sup> (Latham 2009).

The study area is located in the Athabasca bitumen-sands deposits and comprises mostly public lands; however, most of the region has been allocated to forest management agreements and oil and gas extraction leases. Industrial activity increased markedly in the mid- to late-1990s (Tracz et al. 2010), and has impacted approximately 7% of the study area. Industrial activity has resulted in an average of 1.8 km km<sup>-2</sup> of linear developments 100 km<sup>-2</sup> land survey unit (Schneider 2002). Conventional seismic exploration lines are the most pervasive linear development, whereas all-season and seasonal roads and trails, pipeline-right-of-ways, and transmission lines occur at lower densities (Schneider 2002).

## Wolf telemetry data

We assessed resource selection and prey use for eight wolf packs: Algar, Calling, GoCan, Livock, Pelican Lake, Pelican River, and Rock Island (Fig. 1), January 2006–January 2008. We captured wolves in winter by helicopter net-gunning and trapped wolves in summer using modified foot-hold traps (Univ. of Alberta Animal Care and Use Protocol no. 471503). Following the methods described in

Latham et al. (2011a), we attempted to capture and radio-collar ≥ 1 individual in all wolf packs within or bounding the study area. We fitted 12 of 32 captured animals with GPS radiocollars (GPS4400s, LOTTEK, Aurora, ON, Canada) that were programmed with a 2 h relocation schedule: late-April to mid-June (i.e. wolf denning season) 2006 was an exception and we programmed collars with a 45 min relocation schedule. We differentially corrected GPS locations to reduce measurement error (Dussault et al. 2001). Previous trials in Alberta using Lotek GPS collars (with a high number of channels) have demonstrated minimal GPS habitat-induced bias, suggesting that further corrections were unnecessary (Hebblewhite et al. 2007). We defined two seasons, winter (i.e. snow-covered months, October–March) and summer (i.e. months with no permanent snow on the ground, April–September), based on seasonal differences in wolf pack cohesion (Fuller 1989, Latham 2009), strong seasonal caribou mortality bias (McLoughlin et al. 2003), and to ensure appropriate sample sizes in each season.

## Prey covariates

We assessed wolf seasonal spatial resource selection by estimating resource selection functions (RSF) (Manly et al. 2002, Johnson et al. 2006) based on seasonal prey distribution layers, i.e. our models considered those resources that directly contribute to a wolf's survival and reproductive success (Mitchell and Hebblewhite 2012).

Concurrent with the wolf collaring programme, we conducted five fixed-wing aircraft surveys for ungulates during the winters of 2004–2007 (Latham et al. 2011a) and 176 1-km by 2-m ungulate pellet group transects in mid- to late-summer of 2005–2007 (Latham 2009, McPhee et al. 2012). The aerial surveys assessed the relative distribution of visible ungulate species and consisted of east-west transects flown at 1 (ca 1860 m)- or 2-min-of-latitude intervals within a 7000 km<sup>2</sup> portion of the study area that consisted of most of the WSAR range, Athabasca River valley, and adjacent uplands. The pellet group transects were randomly placed in upland and peatland forest-types across the entire study area. Transect direction from the random starting point was based on the cover-type that the random point had been generated in, i.e. if the random point started in a black spruce bog we oriented the transect in a direction that, when possible, fell exclusively in that cover type. Of the 176 transects, 15% were conducted in deciduous forest, 10% in upland conifer forest, 7% in mixed-wood forest, 5% in cut-blocks, 43% in bog, 16% in fen and 5% in burns. We used a simplification of Lehmkuhl et al. (1994) to age pellet groups as fresh (moist or oily texture), old (dry, slightly crusted), or aged (decaying). Because we were only interested in those pellet groups deposited in spring and summer, aged pellet groups were assumed to have been deposited in winter and thus were excluded from analyses.

We modelled ungulate sightings from winter aerial surveys using logistic regression (Hosmer and Lemeshow 2000) to estimate winter RSFs for moose, deer, and caribou separately. We modelled ungulate pellet group sightings using logistic regression to estimate summer RSFs for

moose, deer, and caribou separately. Akaike's information criterion corrected for small samples ( $AIC_c$ ) was used to select between four a priori candidate models (Burnham and Anderson 2002) for each species and season (Supplementary material Appendix 1, Table A1, A2). We constructed each candidate model to reflect hypothesized resource preferences of each species while at the same time avoid parameter over-fitting (as described by Harrell 2001). Explanatory variables included in the ungulate models were: proportion of landcover-type within a 500-m circular buffer (bog, burns, deciduous forest, fen, mixed-wood forest, upland conifer forest, old cutblocks (> 30 yr), middle-aged cutblocks (6–30 yr), young cutblocks (< 6 yr), and water), distance to nearest all-season road (m), distance to the Athabasca river (m), distance to nearest stream (m), distance to nearest upland boundary (m), elevation (m), and linear feature density within a 500-m buffer ( $\text{km km}^{-2}$ ). We chose a 500 m circular buffer to contextualize explanatory variables because this buffer-size has been previously used in large mammal resource selection studies in Alberta (Webb et al. 2008, McPhee et al. 2012). In addition, we included interpolated deer and moose abundance layers as explanatory variables in our deer and moose seasonal RSFs to reflect large-scale patterns in the abundance of these two species. Moose and deer aerial counts and pellet counts were interpolated within  $25 \times 25$  m pixels across the whole study area using inverse-distance weighting ( $1/d^2$ ) (as described by McPhee et al. 2012). We assessed the predictive ability of the top RSF for each ungulate species and season using k-fold cross validation (Boyce et al. 2002). The top RSF models for each prey species were used to generate seasonal resource selection surfaces using ArcGIS ver. 9.3 (ESRI 2008).

The resource selection surface for beaver was estimated using data collected from a fixed-wing aircraft survey of active beaver lodges, October 2007 (Latham 2009). Although beaver availability to wolves may change seasonally (Mech 1966), we assumed that their distribution remained stationary across seasons, which is supported by their fidelity to a fixed landscape feature such as a lodge or river bank den (Lancia and Hodgdon 1984). We modelled beaver lodge sightings using logistic regression to estimate a RSF of beaver lodge occurrence as a function of landcover type within a 500-m buffer (bog, deciduous forest, fen, mixed-wood forest, and water), elevation (m), and distance to nearest stream (m).  $AIC_c$  was used to select between four a priori candidate models (Supplementary material Appendix 1, Table A3) and k-fold cross validation was used to assess predictive ability of the top RSF model.

Species-specific resource selection surfaces were combined to create total prey biomass surfaces for winter and summer separately. To do this, we first converted prey resource selection surfaces to relative density surfaces by using density estimates obtained from aerial surveys conducted within the study area (Stuart-Smith et al. 1997 for caribou:  $4.1/100 \text{ km}^2$ , Alberta Environmental Protection 1998, 2003 for moose:  $17/100 \text{ km}^2$ , Latham 2009 for deer and beaver:  $76.5/100 \text{ km}^2$  and  $154.2/100 \text{ km}^2$ , respectively). Density estimates were used to calculate the number of animals of each species present in our area, which we then spatially distributed across the study area according to

each pixel's RSF score. The relative density surfaces for each species were then summed, weighted by their relative biomass contributions, i.e. moose (6), deer (1), beaver (0.25), and caribou (2) (Keith 1983, Fuller 1989; beaver value is assumed to be a quarter that of an 80 kg deer, Lancia and Hodgdon 1984), to generate a total prey biomass surface in winter and summer separately. In this case, seasonal total prey biomass available to wolves is expressed as deer-sized prey  $625 \text{ m}^{-2}$  pixel.

### Wolf pack resource selection

We assessed selection for areas used by prey at the home range scale for each wolf pack in both summer and winter (i.e. third order selection, sensu Johnson 1980) by comparing prey resource selection values at wolf GPS locations (used) and random (available) locations using RSF. Random locations were sampled at a density of  $1 \text{ km}^{-2}$  of wolf territory (Hebblewhite and Merrill 2008). Wolf territories were estimated as 100% minimum convex polygons (MCP) delimited annually for each wolf pack using an average of 1872 GPS locations (range: 772–3816) per pack. Although competition between packs arising from territorial defence may influence wolf use of territory boundaries (Mech and Boitani 2003), we assumed that all of the area within a 100% MCP was equally available to wolves within a pack. Because many of the interactions between wolves and caribou occur within the distal portion of wolf territories in WSAR and ESAR, we believed that important information about wolf forays into caribou range could be overlooked if we used a 95% MCP or a kernel density estimator. Furthermore, because we were interested in assessing wolf selection for areas used by prey, i.e. hunting behaviour, we excluded GPS locations associated with known wolf den and rendezvous sites (as determined from ground investigations; see Latham 2009 for detailed methods).

We assessed resource selection by wolf packs individually because population-level analyses generally describe the mean pattern of selection within a population and often miss important interactions between individuals and characteristics of their environment (Boyce et al. 2003, Forester et al. 2009). Because we only had one GPS-collared wolf per pack (in all instances breeding adults) we did not need to accommodate for non-independence between wolves within packs as described in Hebblewhite and Merrill (2008). Further, we assessed individual pack resource selection using fixed-effect logistic regression rather than a more complicated multiple random-effects mixed model (as advocated by Murtaugh 2007 for ecological analyses). We developed a set of three a priori candidate models based on our three hypotheses: 1) historic primary prey model, including only moose; 2) common alternative prey model, including deer and beaver; and 3) total prey biomass model. We used  $AIC_c$  to select the top model for each pack and season. We were constrained to use this multi-model approach rather than constructing a single model including all prey variables for each wolf pack because the resource selection surfaces of some of the prey species were highly correlated with each other (Pearson correlation > 0.7). Further, we did not include a caribou model among the candidate models because wolves have been shown to avoid

areas frequented by caribou at the population level (James et al. 2004, Latham 2009); however, to support this claim we also report the selection coefficients from a caribou model. To depict individual-pack responses and average wolf pack-responses, we plotted relative probability of wolf use as a function of changes in the relative probability of use by each prey species in winter and summer. Individual-pack responses were directly predicted using each of the models tested. Average wolf pack-responses were predicted using models constructed from averaging the coefficients for each prey species across packs, i.e. the two-stage modelling approach described by Fieberg et al. (2010) and Northrup et al. (2012). Standard errors around predicted average wolf-pack responses were estimated using bootstrapping.

## Wolf diet

We assessed seasonal wolf prey use via analysis of 397 scats collected from seven packs in early-2006 to early-2008; we were unable to collect scats from the Livock pack because of their remote location (Fig. 1). Scats were collected at GPS location clusters (defined as  $\geq 5$  consecutive locations within 100 m, Anderson and Lindzey 2003) representing wolf kill and resting sites. This method of defining kill sites might underestimate small prey species, thus we also collected scats at den and rendezvous sites. Because we were able to assign approximate dates to each scat, these were grouped into winter ( $n = 113$ ) and summer ( $n = 284$ ). Seasonal scat sample sizes were both larger than the minimum of 94 samples recommended by Trites and Joy (2005) as being required to compare diets over time or between areas. Targeting GPS clusters reduced the likelihood of confusing wolf scats with those of sympatric canid species (coyotes and red foxes). However, if there were no clear tracks associated with a scat to verify species, and the scat was  $< 25$  mm in diameter (Reed et al. 2004) we excluded it from the analysis. Wolf den and rendezvous sites were an exception and we assumed that scats  $< 25$  mm at these locations were from wolf pups.

We randomly selected 20 hairs per scat and identified them to species following Kennedy and Carbyn (1981). Ungulate hairs found in summer scats were further classified into adults or juveniles (Kennedy and Carbyn 1981). In addition, we created a reference set based on hair samples collected from wolf kill sites, hunter and road killed animals. The reference set was used to aid species identification, and to evaluate observer reliability. We could not differentiate between white-tailed deer and mule deer; however, because of the rarity of mule deer in our study area, we assumed all deer remains were from white-tailed deer. The regression method of Weaver (1993) was used to convert percent occurrence in scats to percent of total biomass provided by moose, deer, beaver, and caribou. To do this, we assumed average northeastern Alberta-specific weights of: 400 kg adult moose; 75 kg calf moose; 80 kg adult deer; 25 kg fawn deer; 20 kg beaver; and 140 kg caribou (Lancia and Hodgdon 1984, Renecker and Hudson 1993, Bubenik 1998). Standard errors (SE) around percent occurrence and percent biomass of each prey species in wolf diet were estimated using the binomial confidence estimator (Sokal and Rohlf 1995).

## Predation risk for caribou

We assessed seasonal changes in predation risk for caribou by quantifying wolf use of areas with moderate to high relative probability of caribou use (see below) during winter and summer. We first estimated quantiles by which pixels comprising the winter and summer caribou habitat selection surfaces (see Prey covariates section) were partitioned into five equal-sized subsets. We then reclassified these two surfaces based on these quantiles, establishing five ranks of relative probability of use, i.e. pixels with rank 1 represent areas rarely used by caribou whereas pixels with rank 5 represent areas most frequently used by caribou. We computed the percentage of GPS locations per wolf pack that overlapped areas of moderate to high caribou use (pixels with ranks of relative probability of use of 3, 4 and 5) during winter and summer, and compared these values using a paired t-test (Zar 1996). Finally, we examined the seasonality of 42 radio-collared adult female caribou mortalities that occurred in our study area in 2004–2008. We determined which season radio-collared caribou died in through aerial telemetry flights conducted three to four times per season. In most cases, ground investigations of the dead animals were not conducted. However, we assumed that all caribou mortalities with signs of predator-inflicted injuries or disarticulated skeletons were due to wolves (six confirmed and 36 suspected) because other North American predators that commonly depredate adult caribou do not occur in our study area. We further based this assumption on McLoughlin et al. (2003) who found that  $\sim 75\%$  of adult caribou mortalities in northeastern Alberta could be attributed to predation by wolves, whereas mortalities caused by black bears, coyotes or humans were uncommon or rare.

All statistical analyses were performed in R ver. 2.13.1 for Windows (R Development Core Team).

## Results

### Wolf pack resource selection

We obtained 14018 GPS locations from the eight wolf packs, with 5114 locations in winter and 8904 in summer. During winter aerial surveys, deer observations were most common in uplands ( $72\% \pm 1\%$ ; mean  $\pm$  SE), whereas moose observations were more common in uplands ( $57\% \pm 1\%$ ) than in peatlands ( $43\% \pm 1\%$ ). In summer, deer were most common in uplands ( $71\% \pm 4\%$ ); however, moose observations in peatlands increased markedly ( $67\% \pm 4\%$ ). Beaver lodges were more common in caribou range ( $59\%$ ) than in upland areas adjacent to caribou range ( $41\%$ ). Caribou observations were more abundant in peatlands both in winter ( $80\% \pm 9\%$ ) and summer ( $84\% \pm 10\%$ ).

Ungulate and beaver survey data were used to develop models describing winter and summer resource selection for each ungulate species and annual resource selection for beaver (Supplementary material Appendix 1, Table A1, A2 and A3). The top models performed well based on 5-fold cross-validation (Spearman rank correlation ( $r_s$ ) for moose:  $r_{s \text{ winter}} = 0.83$ ,  $r_{s \text{ summer}} = 0.80$ ; deer:  $r_{s \text{ winter}} = 0.95$ ,

$r_{s \text{ summer}} = 0.99$ ; caribou:  $r_{s \text{ winter}} = 0.97$ ,  $r_{s \text{ summer}} = 0.90$ ; beaver:  $r_{s \text{ annual}} = 0.99$ ; all  $p < 0.001$ ), thus justifying their inclusion as explanatory variables in wolf seasonal RSFs.

The prey species that influenced wolf spatial resource selection in winter showed variation across packs (Table 1). The common alternative prey model was the top model for five packs whereas the historic primary prey model was the top model for the remaining three packs. We found no evidence to support the total prey biomass model for any of the packs, suggesting that wolves did not select resources based solely on prey biomass. Probability of wolf use was positively influenced by areas selected by moose and deer for all wolf packs in winter (Table 2, Fig. 2a). Selection for areas with high probability of use by beaver was more variable with only five packs showing statistically significant positive selection for this variable (Table 2, Fig. 3).

In summer, the common alternative prey model was the top model for six packs (Table 1). Only the Livock pack showed higher support for the historic primary prey model, suggesting that moose continue to drive resource selection for some packs. The total prey biomass model was the top model for the GoCan pack. Summer resource selection by wolves was positively influenced by beaver for seven packs (Table 2, Fig. 2b). Six packs selected areas used by deer whereas these areas were avoided by the remaining two packs (Table 2, Fig. 4). Selection for moose was positive for five packs (Table 2, Fig. 4). However, moose and deer influences on wolf resource selection were not as strong as in winter (Fig. 2a, b).

Most of the packs analysed showed avoidance of areas of high caribou use in both winter and summer (Table 2, Fig. 2a, b). The Rock Island pack was an exception, showing statistically significant selection for areas of high caribou use in both seasons (Fig. 3, 4).

## Wolf diet

During winter, deer were found in 61.1% ( $\pm 4.6\%$ ) of scats and provided 42.6% ( $\pm 4.7\%$ ) of biomass in wolf diet (Fig. 5a, b). Although moose were present in a comparatively low percentage of scats ( $17.7 \pm 3.6\%$ ), they provided a high proportion of biomass ( $41.7 \pm 4.6\%$ ). Beaver were found in 22.1% ( $\pm 3.9\%$ ) of winter scats, accounting for a small percentage of winter biomass ( $8.5 \pm 2.6\%$ ).

Mimicking changes in selection for areas occupied by different prey, wolf diet shifted substantially between seasons. Use of beaver increased in summer when they were found in 58.1% ( $\pm 2.9\%$ ) of scats and constituted 29.8% ( $\pm 2.7\%$ ) of biomass in wolf diet (Fig. 5a, b). White-tailed deer use by wolves declined in frequency ( $32.8 \pm 2.8\%$ ) as well as biomass ( $24.0 \pm 2.5\%$ ). Scats contained adult deer (16.3%) and fawn deer (16.5%). The estimated contribution of moose to wolf diet in summer remained static, but comprised both adult (10.5%) and calf moose (8.5%).

Caribou were rarely found in wolf scats in either winter ( $7.1 \pm 2.4\%$ ) or summer ( $4.2 \pm 1.2\%$ ) (Fig. 5a). Likewise, caribou provided little in terms of biomass in wolf diet during winter ( $7.1 \pm 2.4\%$ ) and summer ( $5.6 \pm 1.4\%$ , Fig. 5b). Only one scat contained hairs from calf caribou. We found that 60% of wolf scats containing caribou ( $n = 20$ ) were from summer (April–September) or 90% using the definition of summer used by McLoughlin et al. (2003) (April–October).

To ensure that commonly sampled packs did not influence our diet results, we randomly selected 10 and 20 scats per wolf pack per season to analyse prey occurrence in wolf diet. These results were similar to those reported above (Supplementary material Appendix 1, Fig. A1).

## Predation risk for caribou

The mean percentage of wolf GPS locations recorded within areas of moderate to high relative probability of caribou use (ranks 3, 4, and 5) was higher in summer ( $38.1\% \pm 6.0\%$ ) than winter ( $24.8\% \pm 5.1\%$ ;  $t_7 = -3.559$ ;  $p = 0.0046$ ). Further, the mean percentage of wolf locations in areas with low probability of caribou use (rank 1) decreased from 61.5% ( $\pm 7.8\%$ ) in winter to 44.3% ( $\pm 7.4\%$ ) in summer (Fig. 6). The mean percentage of wolf locations in areas of high probability of caribou use (rank 5) was low in both winter ( $7.5\% \pm 3\%$ ) and summer ( $8\% \pm 2.8\%$ ), suggesting that regardless of season core peatland areas selected by caribou were not regularly frequented by wolves.

Changing patterns in wolf resource selection and diet were reflected by caribou mortality patterns. Of the 42 adult female caribou mortalities recorded in our study area between 2004 and 2008, 23.8% occurred in winter

Table 1. Akaike weights ( $w_i$ ) providing relative support for each of three logistic regression models used to assess seasonal wolf resource selection. Models were fitted to Global Positioning System data collected from eight wolf packs during winter (October–March) and summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008.

Model <sup>a</sup>	Pack							
	Algar	Calling	GoCan	Joli	Livock	Pelican Lake	Pelican River	Rock Island
Winter								
1. Historic primary prey	0	<b>0.95</b>	<b>1</b>	0	0	0	0	<b>0.85</b>
2. Common alternative prey	<b>1</b>	0	0	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0
3. Total prey biomass	0	0.05	0	0	0	0	0	0.15
Summer								
1. Historic primary prey	0	0	0	0	<b>1</b>	0	0	0
2. Common alternative prey	<b>1</b>	<b>1</b>	0.01	<b>1</b>	0	<b>1</b>	<b>1</b>	<b>1</b>
3. Total prey biomass	0	0	<b>0.99</b>	0	0	0	0	0

<sup>a</sup>Historic primary prey model = moose; common alternative prey model = white-tailed deer + beaver; total prey biomass model = total prey biomass combining moose, white-tailed deer, beaver, and caribou.



Table 2. Standardized selection coefficients ( $\beta$ ) and standard errors (SE) for the three models (Table 1) used to assess seasonal wolf resource selection. Coefficients from a caribou-only model are also presented. Models were fitted to Global Positioning System data collected from eight wolf packs during winter (October–March) and summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008. Values in boldface type indicate statistically significant selection (positive values) or avoidance (negative values) as determined by Wald tests.

Model <sup>a</sup>	Pack								
	Algar	Calling	GoCan	Joli	Livock	Pelican Lake	Pelican River	Rock Island	Average
Winter									
1. Historic primary prey									
Moose									
$\beta$	<b>0.773</b>	<b>0.223</b>	<b>0.522</b>	<b>0.713</b>	<b>0.353</b>	<b>0.713</b>	<b>0.469</b>	<b>0.255</b>	0.503
SE	<b>0.053</b>	<b>0.053</b>	<b>0.038</b>	<b>0.052</b>	<b>0.055</b>	<b>0.053</b>	<b>0.054</b>	<b>0.038</b>	0.049
2. Common alternative prey									
Deer <sup>b</sup>									
$\beta$	<b>0.668</b>	0.057	<b>0.292</b>	<b>1.077</b>	<b>0.728</b>	<b>0.519</b>	<b>0.493</b>	0.053	0.486
SE	<b>0.067</b>	0.046	<b>0.037</b>	<b>0.060</b>	<b>0.058</b>	<b>0.051</b>	<b>0.064</b>	0.053	0.055
Beaver									
$\beta$	<b>0.443</b>	0.070	-0.020	<b>0.416</b>	<b>-0.332</b>	<b>0.638</b>	<b>0.153</b>	<b>0.212</b>	0.198
SE	<b>0.068</b>	0.059	0.041	<b>0.076</b>	<b>0.070</b>	<b>0.061</b>	<b>0.064</b>	<b>0.047</b>	0.061
3. Total prey biomass									
$\beta$	<b>0.851</b>	<b>0.172</b>	<b>0.410</b>	<b>1.058</b>	<b>0.494</b>	<b>0.848</b>	<b>0.509</b>	<b>0.259</b>	0.575
SE	<b>0.053</b>	<b>0.049</b>	<b>0.035</b>	<b>0.056</b>	<b>0.053</b>	<b>0.053</b>	<b>0.057</b>	<b>0.041</b>	0.050
4. Caribou									
$\beta$	<b>-0.479</b>	-0.005	<b>-0.249</b>	<b>-0.951</b>	<b>-0.659</b>	<b>-0.340</b>	<b>-0.780</b>	<b>0.150</b>	-0.414
SE	<b>0.057</b>	0.065	<b>0.037</b>	<b>0.056</b>	<b>0.064</b>	<b>0.044</b>	<b>0.065</b>	<b>0.050</b>	0.055
Summer									
1. Historic Primary Prey									
Moose									
$\beta$	-0.076	<b>0.454</b>	<b>0.585</b>	<b>-0.161</b>	<b>-0.548</b>	<b>0.147</b>	<b>0.121</b>	<b>1.082</b>	0.200
SE	0.042	<b>0.048</b>	<b>0.050</b>	<b>0.040</b>	<b>0.076</b>	<b>0.036</b>	<b>0.036</b>	<b>0.036</b>	0.046
2. Common alternative prey									
Deer <sup>b</sup>									
$\beta$	<b>0.379</b>	<b>-0.290</b>	<b>0.399</b>	<b>0.699</b>	<b>0.549</b>	<b>0.167</b>	<b>0.419</b>	<b>-1.173</b>	0.144
SE	<b>0.057</b>	<b>0.048</b>	<b>0.033</b>	<b>0.055</b>	<b>0.082</b>	<b>0.042</b>	<b>0.041</b>	<b>0.040</b>	0.050
Beaver									
$\beta$	<b>0.485</b>	<b>0.590</b>	<b>0.488</b>	<b>0.504</b>	-0.145	<b>0.269</b>	<b>0.405</b>	<b>0.252</b>	0.356
SE	<b>0.063</b>	<b>0.048</b>	<b>0.036</b>	<b>0.057</b>	0.075	<b>0.047</b>	<b>0.046</b>	<b>0.032</b>	0.050
3. Total prey biomass									
$\beta$	<b>0.341</b>	<b>0.348</b>	<b>0.821</b>	<b>0.504</b>	<b>-0.140</b>	<b>0.205</b>	<b>0.393</b>	<b>0.789</b>	0.408
SE	<b>0.047</b>	<b>0.045</b>	<b>0.050</b>	<b>0.047</b>	<b>0.050</b>	<b>0.036</b>	<b>0.038</b>	<b>0.036</b>	0.044
4. Caribou									
$\beta$	<b>-0.672</b>	0.004	<b>-0.451</b>	<b>-0.831</b>	<b>-0.513</b>	<b>-0.384</b>	<b>-0.426</b>	<b>0.743</b>	-0.316
SE	<b>0.048</b>	0.040	<b>0.029</b>	<b>0.051</b>	<b>0.083</b>	<b>0.047</b>	<b>0.042</b>	<b>0.034</b>	0.047

<sup>a</sup>Historic primary prey model = moose; common alternative prey model = white-tailed deer + beaver; total prey biomass model = total prey biomass combining moose, white-tailed deer, beaver, and caribou; caribou model = caribou.

<sup>b</sup>Deer = white-tailed deer.

(October–March), whereas 76.2% occurred in summer (April–September).

## Discussion

We found that the importance of each prey species in wolf diet varied by season, as did wolf selection for areas used by each prey. Seasonal variation in wolf prey use and selection resulted in contrasting spatial relationships between wolves and caribou. During winter, deer were most abundant in wolf diet and wolves selected areas used by deer, whereas during summer beaver were the most frequently consumed prey species and wolf selection for areas used by beaver increased substantially. Changes in wolf resource selection and diet to target abundant beaver as they became available during summer is consistent with prey switching (Murdoch

1969). Moose were used consistently throughout the year and although they were found infrequently in wolf scat, their large size meant that moose were still important to wolves, representing 40% of biomass consumed by wolves in each season. Based on our seasonal definitions, we found comparable amounts of caribou in wolf diet in winter and summer. However, if we include the cusp month of October into summer, we found that 90% of wolf scats containing caribou were from what are commonly termed snow-free months (McLoughlin et al. 2003). Seasonal differences in prey use by wolves resulted in seasonal contrasts in their use of caribou-preferred habitats, with overlap between wolves and caribou being highest in summer when wolves hunted beaver. Because we also found that most caribou mortalities occurred in summer, it seems plausible that the behavioural response of wolves has resulted in increased predation pressure on caribou through the process of apparent competition.



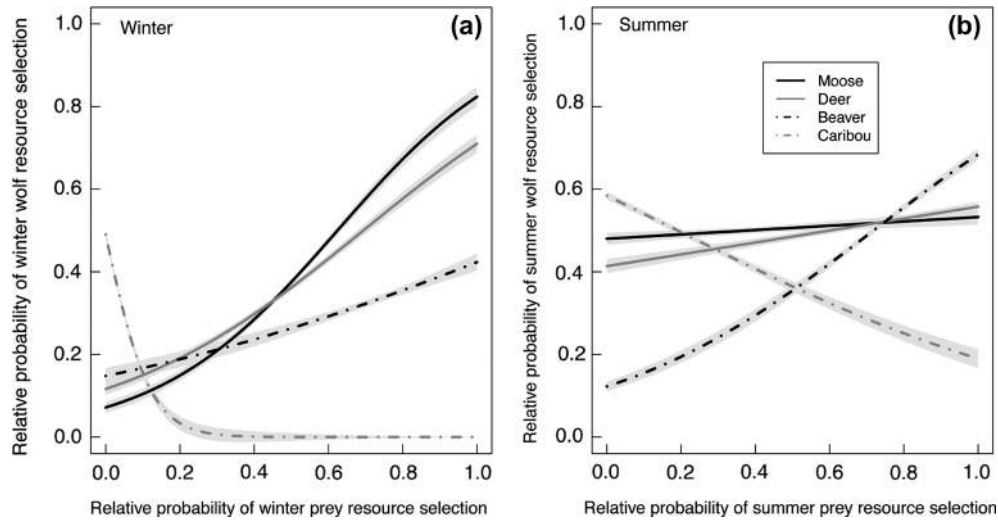


Figure 2. Relative probability of wolf resource selection in (a) winter (October–March) and (b) summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008. Selection probabilities were calculated using the average models presented in Table 2, last column. For each prey species, standard errors (grey envelopes) on the predictions are shown. Wolves showed strong selection for white-tailed deer (deer) and moose and avoidance of caribou in winter, and strong selection for beaver in summer.

Although moose remain important in terms of biomass in wolf diet, they are no longer the most common ungulate prey used by wolves in northeastern Alberta, having been recently replaced by deer (Latham et al. 2011a, Wasser et al. 2011). When moose were the most common prey, wolf preference for moose drew wolves away from prime caribou habitat (Bergerud et al. 1984, James et al. 2004), and this pattern helped explain how caribou coexisted with alternative prey and wolves in the boreal forest, i.e. spatial separation (Bergerud et al. 1984, Seip 1992). Wasser et al. (2011) studied winter (mid-December–mid-March) wolf resource selection and diet in a small portion of the ESAR caribou

range and concluded that wolf preference for deer continues to draw wolves away from prime caribou habitat, reducing the potential for wolves to affect caribou through predation. Although based on a smaller sample of scats, we also found wolf preference for deer during winter. These findings confirm that wolves continue to focus predation and hunting effort outside of core caribou habitat and that caribou are not an important component of wolf diet overall. Thus, some spatial separation between caribou and wolves still occurs in northeastern Alberta and, as in other systems (Wittmer et al. 2005), wolf predation on caribou remains incidental.

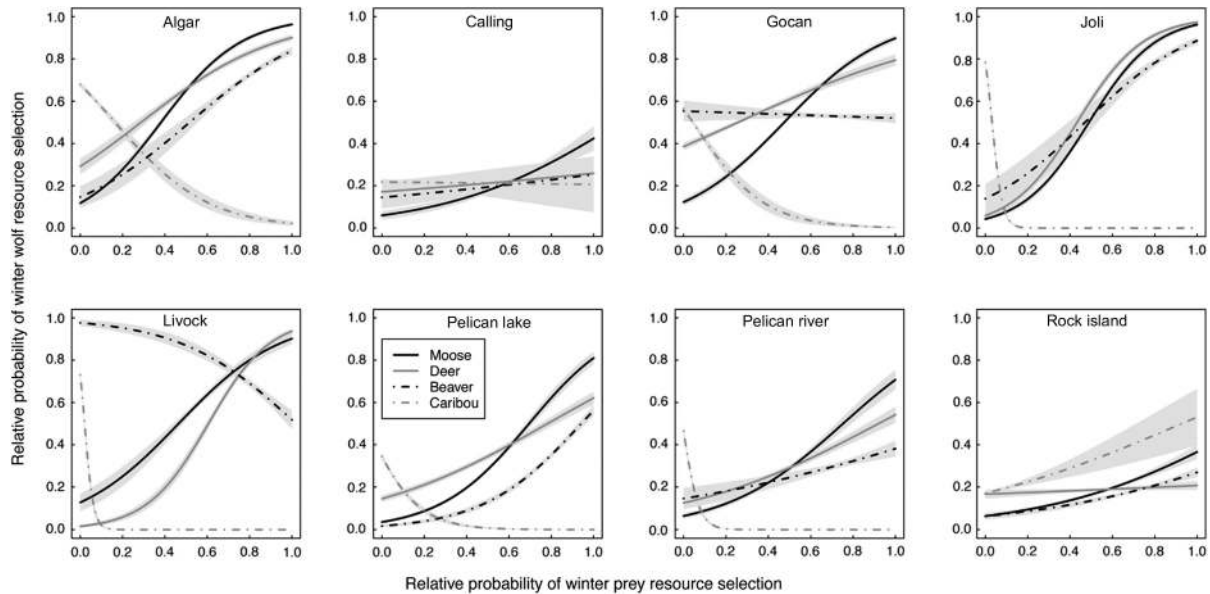


Figure 3. Relative probability of resource selection by eight wolf packs during winter (October–March) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008. Selection probabilities were calculated using the individual wolf pack resource selection models presented in Table 2. For each prey species, standard errors (grey envelopes) on the predictions are shown. Deer = white-tailed deer.

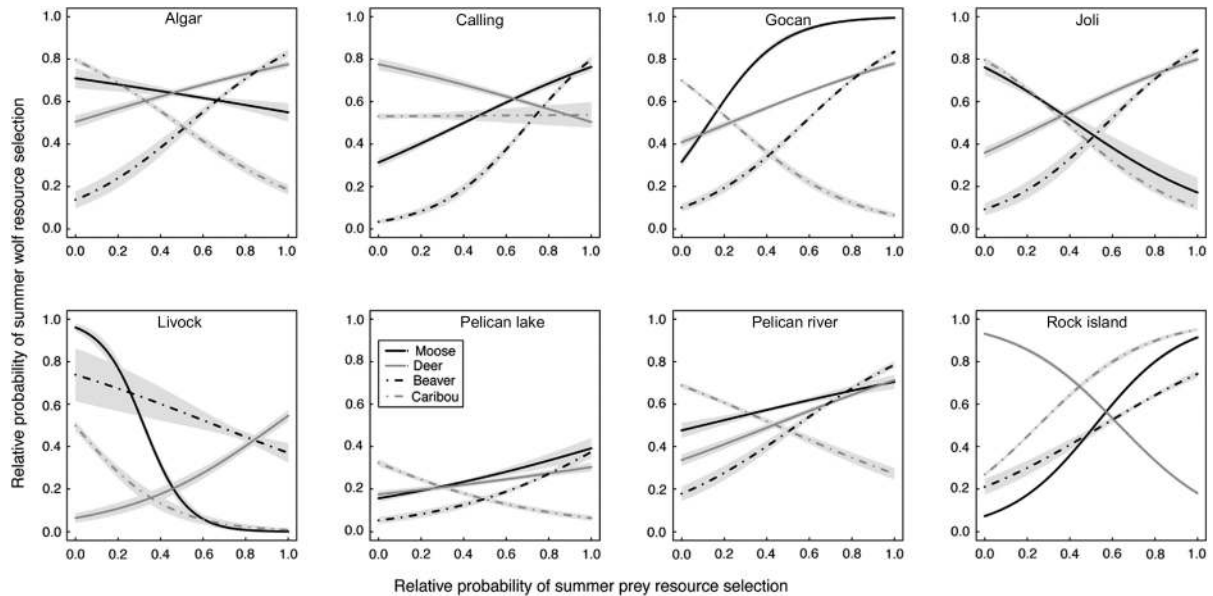


Figure 4. Relative probability of resource selection by eight wolf packs during summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008. Selection probabilities were calculated using the individual wolf pack resource selection models presented in Table 2. For each prey species, standard errors (grey envelopes) on the predictions are shown. Deer = white-tailed deer.

However, recent landscape, climate, and prey community changes appear to be affecting spatial separation, increasing incidental predation of caribou by wolves. While caribou remain an insignificant component of wolf diet overall, their proportion in wolf diet has nevertheless increased substantially in northeastern Alberta in the last decade. Estimates from over-lapping study areas range from a 10-fold increase (Latham et al. 2011a) to a 22-fold increase (Wasser et al. 2011) compared to the tiny proportion of caribou in wolf diet reported by James et al. (2004) in the mid-1990s

(< 1%). The proportional effect of incidental predation on a prey population can be inversely density dependent; that is, mortality increases proportionately as numbers of prey decline (Messier 1994). Moreover, because the numerical response of the predator is the mechanism by which apparent competition affects prey species (Holt et al. 1994), increasing wolf numbers due to prey enrichment (Latham et al. 1994), increasing wolf numbers due to prey enrichment (Latham et al. 2011a) can result in increased incidental encounters and predation events on caribou by wolves (McCutchen 2007). Thus, even though caribou represent a small portion

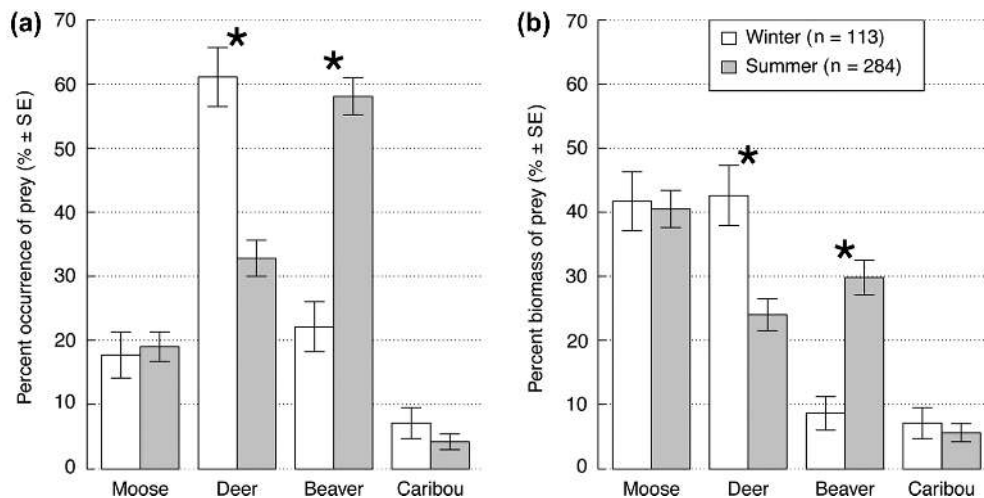


Figure 5. Differences in the diet (determined from prey remains in scats) of wolves between winter (October–March) and summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2007. Values were calculated as (a) percent occurrence and (b) percent biomass in wolf scats (following Weaver 1993). Standard errors around percent occurrence and percent biomass were estimated using the binomial confidence estimator (Sokal and Rohlf 1995). An asterisk indicates statistically significant differences (i.e. non-overlapping 95% confidence intervals) between winter and summer estimates for the species. Note: moose and white-tailed deer (deer) contributions to biomass in summer include a correction to account for moose calf and deer fawn weights.

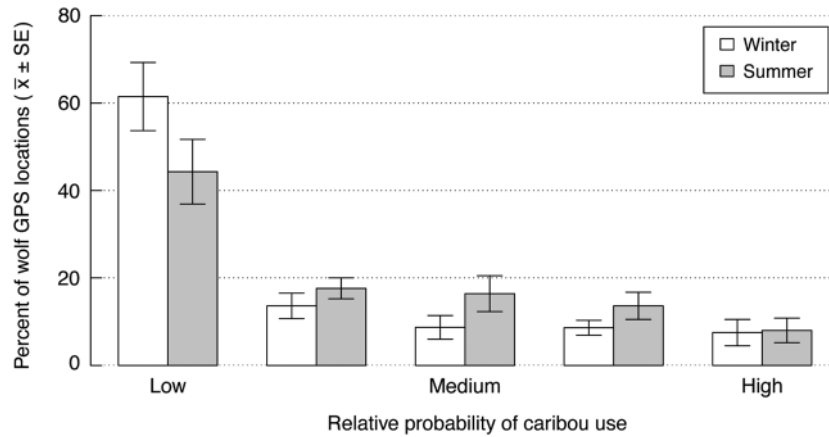


Figure 6. Percent of wolf Global Positioning System locations that overlapped areas of low, medium and high relative probability of use by caribou during winter (October–March) and summer (April–September) in the West and East Sides of the Athabasca River caribou ranges, northeastern Alberta, Canada, 2006–2008. Levels of caribou use were defined by reclassifying seasonal caribou resource selection surfaces into five ranks of relative probability of use (1 = low, 5 = high).

of the diet of wolves and wolf preference for primary prey on average draws wolves away from prime caribou habitat, incidental predation by wolves could still drive caribou population declines (McLoughlin et al. 2003, Wittmer et al. 2005, Latham et al. 2011a).

Our results contribute to the growing acknowledgment of the importance of year-round studies for understanding large mammal predator–prey systems (Sand et al. 2008, Knopff et al. 2010, Metz et al. 2012). We found that seasonal differences in prey use and strength of spatial selection resulted in complex spatiotemporal relationships between wolves and caribou. Most noticeably, our results show increased wolf use of caribou-preferred habitats in summer when wolves switched from deer to beaver, suggesting the potential mechanism (i.e. seasonal prey switching) behind why most caribou in northeastern Alberta (McLoughlin et al. 2003) and elsewhere in western North America and northern Europe (Seip 1992, Kojola et al. 2004, Whittington et al. 2011) are killed by wolves during summer and early-autumn. Although we could not confirm that wolves killed all of the adult caribou mortalities that we recorded, we still found seasonal caribou mortality patterns matching those of McLoughlin et al. (2003), suggesting that wolves remain the most important mortality factor. Moose also are commonly associated with wet meadows in peatlands during summer (Osco et al. 2004), and the positive association with moose that we identified for some packs may contribute to increased wolf overlap with caribou in summer. While spatial separation considered on an annual basis persists, it is reduced by seasonal prey use and selection.

In addition to reduced spatial separation between wolves and caribou during summer, changes in wolf hunting behaviour at that time of year may increase encounter rates with caribou. Wolf packs are less likely to hunt as cohesive units during spring and summer (Fuller 1989, Latham 2009), increasing the number of wolf hunting units on the landscape. Ignoring the effect of season on wolf–caribou dynamics could lead to misguided inference and poor decision making. Studies conducted only in summer may overestimate the effect of wolves on caribou, whereas studies conducted

only in mid-winter (Wasser et al. 2011) are likely to underestimate it.

Beaver were an important driver of seasonal changes in wolf resource selection and reduced spatial separation with caribou during summer (i.e. behavioural response of the predator), and beaver may also contribute to overall prey enrichment and the demographic response by wolves in our area. Beaver are important prey for wolves in many parts of North America (Mech 1966, Messier and Crête 1985), but beaver consumption by wolves in northeastern Alberta has not been high since they were extirpated and reintroduced in the mid-1900s (Martell et al. 2006). We found much higher rates of beaver consumption than have been reported previously (Fuller and Keith 1980, James et al. 2004). The reasons for this are unclear. One plausible explanation is that beaver populations have been increasing since their reintroduction. Whatever the cause of the observed change, our results highlight the importance of a small but abundant non-ungulate prey for incidental predation and apparent competition in a large mammal predator–prey community.

Although most beaver consumption by wolves occurred during summer, we also found some beaver in winter scats. However, over half of these scats were from spring (36%) and autumn (24%), i.e. cusp months, as opposed to winter (December–February). Similarly, we found that many of the scats containing caribou were collected in October (a winter month according to our seasonal definition). Both of these results suggest that the months that are transitional between our definitions of winter and summer are also important in terms of wolf use of peatlands and spatial overlap with caribou. Further, this highlights the challenge of identifying ecologically meaningful seasons in multi-prey systems when different prey species may experience different seasonal vulnerability to predation. For example, Basille et al. (2012) showed that there were important differences between seasonal vulnerability to predation and overlap between caribou and moose, which would only be more complicated in our system with four prey species. Understanding the seasonality of vulnerability to predation in multi-prey systems remains an important question for

declining caribou species in systems affected by apparent competition.

We found no support for the total biomass hypothesis, i.e. that wolves show generalist hunting patterns by selecting for areas with highest total available prey regardless of species. However, this result should be taken cautiously given some of the challenges associated with estimating prey availability over large landscapes. We used aerial surveys in winter and fecal pellet transects in summer to estimate seasonal prey distribution. Both survey methods suffer from detection biases and, in the case of fecal pellets, potentially variable decomposition rates between habitat types (Lehmkuhl et al. 1994, Vander Wal et al. 2011). Despite these biases, we remain convinced our inferences are correct. First, winter aerial surveys are likely to be biased towards underestimating deer in uplands because of closed-canopy forested stands; although we did not correct for this detection bias, we still found that wolves selected for deer in uplands during winter. Second, fecal pellets may decompose more quickly in peatlands because the water-table is at or near the surface in this habitat (Lehmkuhl et al. 1994, but see Webb 2009 who found no differences in pellet detection rates across similar habitat types to those in our study area), potentially overestimating ungulate prey in uplands compared to peatlands in summer. Despite these biases, wolves still selected areas used by prey species in peatlands during summer, resulting in increased use of caribou-preferred habitats. Another potential limitation is the coarse approach that we used to calculate total prey biomass, i.e. we did not account for the proportion of calves, yearlings, and adults in the population of each prey species. By assuming an adult-biased weight value for the contribution of each prey species we probably overestimated total prey biomass available to wolves. Despite this, we found no support for the total prey biomass hypothesis, suggesting that we would find even less support for this hypothesis if we had corrected for younger animals. Finally, because we only used one spatial scale (i.e. within a 500-m buffer) to contextualize habitat variables, we may have overlooked important attributes that influence resource selection behaviour at local or larger landscape scales (Leblond et al. 2011, Lesmerises et al. 2012). However, even though we did not assess resource selection hierarchically, our seasonal prey models performed well based on 5-fold cross-validation (all  $r_s > 0.8$ ), supporting their robustness in predicting prey behaviour and distribution.

Our results also highlight the potential for population-level analyses to obscure additional important features of a predator-prey system. When averaged across a population, resource selection and spatial overlap studies often report that predators select different habitats to incidental prey such as caribou (James et al. 2004). As a consequence, they might miss important interactions between individual predators and characteristics of their home range (Boyce et al. 2003, Forester et al. 2009), such as individual differences in spatiotemporal relationships with prey (Latham et al. 2011c) or in prey selection patterns (Knopff 2010). For example, we found that most wolf packs showed strong selection for beaver in summer, but that some packs continued to select areas used by deer. These differences can have

important implications for caribou because wolf selection for one prey, beaver, resulted in increased spatial overlap between wolves and caribou. Furthermore, our individual-level analyses showed that although most wolf packs avoided caribou, one pack (Rock Island) selected areas used by caribou. Spatial or temporal limitations in data collection might result in an inability to detect differences in individual wolf pack specialization and consequently the impact of wolves on caribou populations.

Our findings do not negate the importance of other factors such as habitat degradation and loss or anthropogenic activities that have been implicated in caribou population declines (Schneider et al. 2010, Festa-Bianchet et al. 2011). Indeed, recent industrial activity has an important influence on spatiotemporal predator-prey relationships in the region. For example, Latham et al. (2011b) reported a seasonal effect whereby wolf use of industrial linear features as travel corridors into peatlands increased in summer and resulted in wolves hunting more frequently in caribou-preferred habitats (also see James and Stuart-Smith 2000). Further, increasing populations of alternative predators have also been identified as important factors behind caribou population declines, e.g. low calf survival because of black bear predation in some parts of eastern Canada (Pinar et al. 2012), or increased predation risk for caribou because of individual variation in black bear selection for caribou-preferred habitats (Latham et al. 2011c). Thus, we contend that a complex combination of biotic and abiotic factors have resulted in changes in the spatial relationships between alternative prey, caribou, and their shared predator, wolves. The consequence of these changes in our system has been an increase in incidental predation by wolves on caribou, particularly in summer. The seasonal shifts in wolf resource use and predation patterns we report here coincide with adult caribou mortality patterns, supporting the conclusion that wolves adversely affect woodland caribou and wild reindeer populations throughout much of their western North American and European range (Bergerud 1974, Seip 1992, Kojola et al. 2004, Wittmer et al. 2005, Gustine et al. 2006, Festa-Bianchet et al. 2011, Latham et al. 2011a, Serrouya et al. 2011). Although politically challenging, we recommend that, if caribou are to be preserved in systems that have undergone prey enrichment and landscape change, wolf (and possibly alternative predator) and alternative prey management be included in the three-pronged approach to caribou conservation suggested by Schneider et al. (2010) and Wittmer et al. (2013).

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## References

- Alberta Environmental Protection 1998. Northern moose management program progress report. – Report for Alberta Environmental Protection, Edmonton, AB, Canada.
- Alberta Environmental Protection 2003. Moose survey in WMU 511 February 11–17, 2003. – Report for Alberta Environmental Protection, Edmonton, AB, Canada.
- Anderson, C. R. and Lindzey, F. G. 2003. Estimating cougar predation rates from GPS location clusters. – *J. Wildl. Manage.* 67: 307–316.
- Basille, M. et al. 2012. Ecologically based definition of seasons clarifies predator–prey interactions. – *Ecography*. doi: 10.1111/j.1600-0587.2011.07367.x
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. – *J. Wildl. Manage.* 38: 757–770.
- Bergerud, A. T. 1985. Antipredator strategies of caribou: dispersion along shorelines. – *Can. J. Zool.* 63: 1324–1329.
- Bergerud, A. T. et al. 1984. Antipredator tactics of calving caribou: dispersion in mountains. – *Can. J. Zool.* 62: 1566–1575.
- Boisjoly, D. et al. 2010. Coyote habitat selection and management implications for the Gaspésie caribou. – *J. Wildl. Manage.* 74: 3–11.
- Boutin, S. et al. 2012. Why are caribou declining in the oil sands? – *Front. Ecol. Environ.* 10: 65–67.
- Boyce, M. S. et al. 2002. Evaluating resource selection functions. – *Ecol. Model.* 157: 281–300.
- Boyce, M. S. et al. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. – *Ecoscience* 10: 421–431.
- Bubenik, A. B. 1998. Evolution, taxonomy and morphophysiology. – In: Franzmann, A. W. and Schwartz, C. C. (eds), *Ecology and management of the North American moose*. A Wildlife Management Institute Book, pp. 77–123.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Chaneton, E. J. and Bonsall, M. B. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. – *Oikos* 88: 380–394.
- Côte, S. D. et al. 2004. Ecological impacts of deer overabundance. – *Annu. Rev. Ecol. Evol. Syst.* 35: 113–147.
- Cumming, H. G. 1992. Woodland caribou: facts for forest managers. – *For. Chron.* 68: 481–491.
- Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada. – PhD thesis, Dept of Biol. Sci., Univ. of Alberta, Edmonton, AB, Canada.
- DeCesare, N. J. et al. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. – *Anim. Conserv.* 13: 353–362.
- Dussault, C. et al. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. – *Wildl. Soc. Bull.* 29: 171–179.
- ESRI 2008. ArcGIS: release 9.3 edition [computer program]. – Environmental Systems Research Inst. (ESRI), Redlands, California.
- Festa-Bianchet, M. et al. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. – *Can. J. Zool.* 89: 419–434.
- Fieberg, J. et al. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity. – *Phil. Trans. R. Soc. B* 365: 2233–2244.
- Forester, J. D. et al. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. – *Ecology* 90: 3554–3565.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. – *Wildl. Monogr.* 105: 1–41.
- Fuller, T. K. and Keith, L. B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. – *J. Wildl. Manage.* 44: 583–602.
- Gleeson, S. K. and Wilson, D. S. 1986. Equilibrium diet: optimal foraging and prey coexistence. – *Oikos* 46: 139–144.
- Gustine, D. D. et al. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. – *Wildl. Monogr.* 165: 1–32.
- Harrell, F. E. Jr 2001. Regression modelling strategies: with applications to linear models, logistic regression, and survival analysis. – Springer.
- Hebblewhite, M. and Merrill, E. 2008. Modelling wildlife–human relationships for social species with mixed-effects resource selection models. – *J. Appl. Ecol.* 45: 834–844.
- Hebblewhite, M. et al. 2007. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. – *J. Wildl. Manage.* 71: 2026–2033.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – *Theor. Popul. Biol.* 12: 197–229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. – *Am. Nat.* 124: 377–406.
- Holt, R. D. and Kotler, B. P. 1987. Short-term apparent competition. – *Am. Nat.* 130: 412–430.
- Holt, R. D. et al. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. – *Am. Nat.* 144: 741–771.
- Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley.
- James, A. R. C. and Stuart-Smith, A. K. 2000. Distribution of caribou and wolves in relation to linear corridors. – *J. Wildl. Manage.* 64: 154–159.
- James, A. R. C. et al. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. – *J. Wildl. Manage.* 68: 799–809.
- Johnson, C. J. et al. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. – *J. Wildl. Manage.* 70: 347–357.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – *Ecology* 61: 65–71.
- Keith, L. B. 1983. Population dynamics of wolves. – In: Carbyn, L. N. (ed.), *Wolves in Canada and Alaska: their status, biology, and management*. Report Series no. 45, Canadian Wildlife Service, pp. 66–77.
- Kennedy, A. J. and Carbyn, L. N. 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian national parks. – Canadian Wildlife Service, Edmonton, AB, Canada.
- Knopff, K. H. 2010. Cougar predation in a multi-prey system in west-central Alberta. – PhD thesis, Dept of Biol. Sci., Univ. of Alberta, Edmonton, AB, Canada.
- Knopff, K. H. et al. 2010. Cougar kill rate and composition in a multiprey system. – *J. Wildl. Manage.* 74: 1435–1447.
- Kojola, I. et al. 2004. Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. – *J. Zool.* 263: 229–235.
- Lancia, R. A. and Hodgdon, H. E. 1984. Beavers. – In: Macdonald, D. (ed.), *The encyclopedia of mammals*. Equinox, pp. 606–609.
- Latham, A. D. M. 2009. Wolf ecology and caribou–primary prey–wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. – PhD thesis, Dept of Biol. Sci., Univ. of Alberta, Edmonton, AB, Canada.
- Latham, A. D. M. et al. 2011a. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. – *J. Wildl. Manage.* 75: 204–212.

- Latham, A. D. M. et al. 2011b. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. – *Ecol. Appl.* 21: 2854–2865.
- Latham, A. D. M. et al. 2011c. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. – *Can. J. Zool.* 89: 267–277.
- Leblond, M. et al. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. – *Landscape Ecol.* 26: 1433–1446.
- Lehmkuhl, J. F. et al. 1994. Elk pellet-group decomposition and detectability in coastal forests of Washington. – *J. Wildl. Manage.* 58: 664–669.
- Lesmerises, F. et al. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. – *For. Ecol. Manage.* 276: 125–131.
- Manly, B. F. J. et al. 2002. Resource selection by animals: statistical design and analysis for field studies. – Kluwer.
- Martell, K. A. et al. 2006. Riparian disturbance due to beavers (*Castor canadensis*) in Alberta's boreal mixedwood forests: implications for forest management. – *Ecoscience* 13: 164–171.
- McCutchen, N. A. 2007. Factors affecting caribou survival in northern Alberta: the role of wolves, moose, and linear features. – PhD thesis, Dept of Biol. Sci., Univ. of Alberta, Edmonton, AB, Canada.
- McLoughlin, P. D. et al. 2003. Declines in populations of woodland caribou. – *J. Wildl. Manage.* 67: 755–761.
- McLoughlin, P. D. et al. 2005. Relating predation mortality to broad-scale habitat selection. – *J. Anim. Ecol.* 74: 701–707.
- McPhee, H. M. et al. 2012. Time-to-kill: measuring attack rates in a heterogeneous landscape with multiple prey types. – *Oikos* 121: 711–720.
- Mech, L. D. 1966. The wolves of Isle Royale, U.S. – National Park Service Fauna Series no. 7, U.S. Government Printing Office, Washington DC.
- Mech, L. D. and Boitani, L. 2003. Wolf social ecology. – In: Mech, L. D. and Boitani, L. (eds), *Wolves: behavior, ecology, and conservation*. Univ. of Chicago Press, pp. 1–34.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. – *Ecology* 75: 478–488.
- Messier, F. and Crête, M. 1985. Moose–wolf dynamics and the natural regulation of moose populations. – *Oecologia* 65: 503–512.
- Metz, M. C. et al. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. – *J. Anim. Ecol.* 81: 553–563.
- Mitchell, M. S. and Hebblewhite, M. 2012. Carnivore habitat ecology: integrating theory and application for conservation. – In: Powell, R. A. and Boitani, L. (eds), *Carnivore ecology and conservation: a handbook of techniques*. Oxford Univ. Press, pp. 218–255.
- Müller, C. B. and Godfray, H. C. J. 1997. Apparent competition between two aphid species. – *J. Anim. Ecol.* 66: 57–64.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. – *Ecol. Monogr.* 39: 335–354.
- Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. – *Ecology* 88: 56–62.
- Northrup, J. M. et al. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. – *J. Anim. Ecol.* 49: 1159–1167.
- Osko, T. J. et al. 2004. Moose habitat preferences in response to changing availability. – *J. Wildl. Manage.* 68: 576–584.
- Pinard, V. et al. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. – *J. Wildl. Manage.* 76: 189–199.
- Reed, J. E. et al. 2004. Differentiating Mexican gray wolf and coyote scats using DNA analysis. – *Wildl. Soc. Bull.* 32: 685–692.
- Renecker, L. A. and Hudson, R. J. 1993. Morphology, bioenergetics and resource use: patterns and processes. – In: Stelfox, J. B. (ed.), *Hoofed mammals of Alberta*. Lone Pine Publishing, pp. 141–163.
- Roemer, G. W. et al. 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. – *Proc. Natl Acad. Sci. USA* 99: 791–796.
- Roughgarden, J. and Feldman, M. 1975. Species packing and predation pressure. – *Ecology* 56: 459–492.
- Sand, H. et al. 2008. Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates? – *Oecologia* 156: 53–64.
- Schmidt, K. A. 2004. Incidental predation, enemy-free space and the coexistence of incidental prey. – *Oikos* 106: 335–343.
- Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. – *Ecology* 68: 1887–1897.
- Schneider, R. R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. – The Federation of Alberta Naturalists and The Alberta Centre for Boreal Research.
- Schneider, R. R. et al. 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. – *Biol. Conserv.* 143: 1603–1611.
- Schramm, T. 2005. Woodland cree traditional environmental knowledge of critical ungulate habitat in the caribou mountains. – PhD thesis, Dept of Renewable Resources, Univ. of Alberta, Edmonton, AB, Canada.
- Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. – *Can. J. Zool.* 70: 1494–1503.
- Serrouya, R. et al. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. – *J. Appl. Ecol.* 48: 935–942.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. – W. H. Freeman.
- Stuart-Smith, A. K. et al. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. – *J. Wildl. Manage.* 61: 622–633.
- Tracz, B. V. et al. 2010. Annual and monthly range fidelity of female boreal woodland caribou in response to petroleum development. – *Rangifer* 30: 31–44.
- Trites, A. W. and Joy, R. 2005. Dietary analysis from fecal samples: how many scats are enough? – *J. Mammal.* 86: 704–712.
- Vander Wal, E. et al. 2011. Spatial and temporal factors influencing sightability of elk. – *J. Wildl. Manage.* 75: 1521–1526.
- Vitt, D. H. 1994. An overview of factors that influence the development of Canadian peatlands. – *Mem. Entomol. Soc. Can.* 169: 7–20.
- Vors, L. S. and Boyce, M. S. 2009. Global declines of caribou and reindeer. – *Global Change Biol.* 15: 2626–2633.
- Wasser, S. K. et al. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. – *Front. Ecol. Environ.* 9: 546–551.
- Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. – *J. Wildl. Manage.* 57: 534–538.
- Webb, N. F. 2009. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. – PhD thesis, Dept of Biol. Sci., Univ. of Alberta, Edmonton, AB, Canada.

- Webb, N. F. et al. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. – *J. Wildl. Manage.* 72: 798–807.
- Whittington, J. et al. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. – *J. Appl. Ecol.* 48: 1535–1542.
- Wittmer, H. U. et al. 2005. The role of predation in the decline and extirpation of woodland caribou. – *Oecologia* 144: 257–267.
- Wittmer, H. U. et al. 2013. Conservation strategies for species affected by apparent competition. – *Conserv. Biol.* doi: 10.1111/cobi.12005
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd ed. – Prentice-Hall.

Supplementary material (Appendix ECOG-00035 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1.