

Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta¹

Andrea D. KORTELO², Department of Fish and Wildlife, University of Idaho, Moscow, Idaho 83844-1136, USA.

Thomas E. HURD, Banff National Park Wildlife Lab, Box 900, Banff, Alberta T1L 1K2, Canada.

Dennis L. MURRAY, Department of Biology, Trent University, Peterborough, Ontario K9J 7B8, Canada.

Abstract: Large carnivore populations are recovering in many protected areas in North America, but the effect of increasing carnivore numbers on existing predator–prey and predator–predator interactions is poorly understood. We studied diet and spatial overlap among cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta (1993–2004) to evaluate how wolf recovery in the park influenced diet choice and space use patterns of resident cougars. Cougars ($n = 13$) and wolves ($n = 8$ in 2 packs) were monitored intensively over 3 winters (2000–2001 to 2002–2003) via radio telemetry and snowtracking. We documented a 65% decline in the local elk population following the arrival of wolves, with cougars concurrently switching from a winter diet primarily constituted of elk to one consisting mainly of deer and other alternative prey. Elk also became less important in wolf diet, but this latter diet switch lagged 1 y behind that of cougars. Wolves were responsible for cougar mortality and usurping prey carcasses from cougars, but cougars failed to exhibit reciprocal behaviour. Cougar and wolf home ranges overlapped, but cougars showed temporal avoidance of areas recently occupied by wolves. We conclude that wolves can alter the diet and space use patterns of sympatric large carnivores through interference and exploitative interactions. Understanding these relationships is important for the effective conservation and management of large mammals in protected areas where carnivore populations are recovering.

Keywords: avoidance, *Canis lupus*, diet, interference, *Puma concolor*.

Résumé : Les populations de grands carnivores sont en voie de rétablissement dans plusieurs aires protégées d'Amérique du Nord. Cependant, l'effet de l'augmentation du nombre de carnivores sur les interactions existantes entre les prédateurs et leurs proies ainsi qu'entre les différents prédateurs ne sont pas bien comprises. Nous avons étudié la diète et le chevauchement spatial entre les cougars (*Puma concolor*) et les loups gris (*Canis lupus*) dans le parc national de Banff en Alberta (1993–2004) afin d'évaluer comment le rétablissement des loups dans le parc a influencé le choix de diète et l'utilisation de l'espace chez les cougars résidents. Treize cougars et 8 loups (de 2 meutes) ont été suivis de façon intensive durant 3 hivers (2000–2001 à 2002–2003) par télémétrie radio et suivi de pistes dans la neige. Suite au retour des loups, nous avons documenté un déclin de 65 % dans la population locale de wapitis et en même temps une modification de la diète hivernale des cougars qui était composée principalement de wapitis vers une diète majoritairement tournée vers les cerfs et d'autres proies alternatives. L'importance des wapitis dans la diète des loups a aussi diminuée mais ce changement s'est opéré un an plus tard chez les loups par rapport aux cougars. Les loups étaient responsables de mortalité chez les cougars et d'usurpation de carcasses de leurs proies mais le comportement réciproque n'a pas été observé chez les cougars. Les domaines vitaux des cougars et des loups se chevauchaient mais les cougars démontraient un évitement temporel des aires récemment occupées par les loups. Nous concluons que les loups peuvent causer un changement dans la diète et dans les patrons d'utilisation de l'espace chez des grands carnivores sympatriques par des interactions d'interférence et d'exploitation. Il est donc important de comprendre ces relations pour la conservation et une gestion efficace des grands mammifères dans les aires protégées où les populations de carnivores sont en voie de rétablissement.

Mots-clés : *Canis lupus*, diète, évitement, interférence, *Puma concolor*.

Nomenclature: Nowak, 1999.

Introduction

Interactions between large carnivore populations can be of critical relevance to community structure, conservation biology, and wildlife management (Creel & Creel, 1996; Durant, 1998; Linnell & Strand, 2000). However, understanding the interactions between large carnivores is

particularly challenging because of the low densities, large spatial requirements, and cryptic behaviour exhibited by most species and the difficulty of manipulating their population densities experimentally. Opportunities to explore the dynamics of such relationships may occur after unintended natural experiments that result from species recolonization or range expansion (Litvaitis & Harrison, 1989; Sinclair, 1991; Arjo & Pletscher, 1999; Thornton, Sunquist & Main, 2004). However, an emphasis on static measures of niche overlap (Witmer & deCalesta, 1986; Fedriani, Palomares & Delibes, 1999; Elmhagen, Tannerfeldt & Angerbjörn, 2002)

¹Rec. 2006-02-22; acc. 2006-12-21.

Associate Editor: Douglas Morris.

²Author for correspondence. Present address: Banff National Park Wildlife Lab, Box 900, Banff, Alberta T1L 1K2, Canada, e-mail: kortello@yahoo.com

has hampered conclusive analyses of competitive interactions between carnivores.

Recently, wolf (*Canis lupus*) populations have increased across much of their historical range in North America, either due to intended translocation or natural recolonization (Bangs *et al.*, 1998). Cougar (*Puma concolor*) distribution is widespread across much of the expanded wolf distribution, and sympatric wolves and cougars are known to share home ranges, habitat, and prey (Kunkel *et al.*, 1999; Duke, 2001; Husseman *et al.*, 2003; Ruth, 2004). Accordingly, cougars and wolves may be subject to agonistic or exploitative interactions, leading to declines or suppression of one or both species. In theory, exploitative competition depends on the capacity of a consumer to deplete shared resource levels (Holt, Grover & Tilman, 1994), and evidence of such requires an understanding of prey abundance and respective prey use patterns (*e.g.*, see Kunkel & Pletscher, 1999). However, wolves may also kill cougars or usurp their prey carcasses (Boyd & Neale, 1992; Kunkel *et al.*, 1999; Palomares & Caro, 1999; Ruth 2004), implying that agonistic interactions between the 2 species also may occur and be asymmetric in favour of wolves. However, if deleterious interactions between predators are rare, or if cougars readily compensate by exploiting alternate food sources or habitats that are unoccupied by wolves, then the effects of competition with wolves may be limited.

We studied sympatric cougars and wolves over 3 winters in Banff National Park, Alberta, to evaluate the prevalence and intensity of their exploitative and agonistic interactions. Extirpated from the park in the mid 1950s (Paquet, 1993), wolves have recently recolonized portions of the park, whereas cougars have maintained a continuous presence since earliest historical records (Holroyd & Van Tighem, 1983). We predicted that diet composition of the 2 predators would diverge as wolf populations became established and prey abundance became limited, which would suggest that exploitative interactions occurred between the 2 species. Evidence of wolves either killing cougars or appropriating their food resources would suggest interference competitive interactions. Consequent to the alleged asymmetry in competitive abilities between the 2 predators, we also predicted that cougars would avoid wolves across a range of spatial scales.

Methods

STUDY AREA

We conducted this study in Banff National Park (BNP) and nearby public lands, in southwestern Alberta, Canada (51° 10' N, 115° 34' W). The main study area was in the Bow Valley, approximately 85 km in length and 4 km wide between Canmore and Lake Louise, and included the townsite of Banff. The average winter (December–February) temperature was –7.5 °C, with annual snowfall averaging 250 cm but snow accumulation rarely exceeding 50 cm in the valley bottom (Huggard, 1993). Throughout the winter, chinook winds caused occasional warmer weather and snow-free periods. Lower elevation vegetation was characterized by lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga menziesii*) forests, aspen (*Populus tremuloides*) parkland,

and grassland interspersed with willow (*Salix* sp.) riparian communities. At higher elevations, Englemann spruce/sub-alpine fir (*Abies lasiocarpa*) forests were predominant, mixed with avalanche terrain containing small shrubs and forbs. This habitat gradually gave way to alpine meadows and rock cover above 2300 m, with the latter habitat not used by either cougars or wolves in winter. Major predators in the area also included grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*). Wolves began to recolonize the area in the mid 1980s. However, they were allegedly excluded from the central Bow Valley by high human use (Paquet, Wierzchowski & Callaghan, 1996) until 1999. Elk (*Cervus elaphus*) were the most abundant ungulate in the study area. Other prey species included white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) at lower elevations and bighorn sheep (*Ovis canadensis*) at higher elevations. Moose (*Alces alces*) and mountain goat (*Oreamnos americanus*) were rare.

MONITORING OF CARNIVORES AND UNGULATES

We conducted the main portion of the study over the winters (November–April) of 2000–2001 to 2002–2003, with supplementary data on wolf and cougar space use collected between 1993 and 1999. During the main study period, cougars were first detected from tracks in the snow and subsequently chased and treed using hounds. To achieve immobilization, we administered a mixture of ketamine (Vetalar™) and medetomidine (Zalopine™), using a dart gun. This combination allowed reversible anaesthesia using atipamezole (Antisedan™) (Kreeger, 1999). Animals received either a VHF (Lotek Engineering, Newmarket, Ontario, Canada) or GPS (Televilt International, Ramsberg, Sweden) radio-collar, with GPS collars deployed principally in 2001 and 2002. We live-trapped and radio-collared wolves with VHF collars as described by Hebblewhite, Pletscher, and Paquet (2002). The University of Idaho Animal Care and Use Committee (No. 2002-20) approved our capture and handling protocol.

Throughout the winter, we continued to check for unknown cougar or wolf tracks in snow approximately once per week, using transects across the valley. Due to the intensity of our field efforts and the restricted size of habitat potentially usable by predators in our study area, we are confident that during our study all resident cougars and a sample of individuals from all resident wolf packs were monitored by telemetry.

We attempted to locate radio-collared animals at least once per day via ground telemetry, and we sought to locate sympatric pairs of cougars and wolves within the same 2-h period whenever possible. Animals on a kill were subject to more intensive telemetry (*i.e.*, 3–6 locations over a 24-h period), which enabled us to monitor possible displacement by heterospecifics. Additionally, GPS collars were programmed for 12 locations per day at 2-h intervals. Using a protocol developed by Jacobson and Kunelius (1985), we surveyed elk populations by helicopter during April or May of each year. Sightability assessment (Hebblewhite, 2000) suggests that roughly 11% of the population was not observed during any given count, implying that surveys were sufficiently precise to detect relatively large annual changes in elk numbers. Additionally, we surveyed 1812

(1000 × 2 m) replicate transects for ungulate pellet group counts during May and June in 1997, 2001, and 2003 to determine the relative abundance of elk and alternative ungulate prey. Only winter pellet groups were counted. Transects were stratified by habitat type (Holland & Coen, 1982) and ran perpendicular to the valley orientation.

KILLS

Throughout the winter, we snow-tracked cougars (2000–2001: 211 km; 2001–2002: 214 km; 2002–2003: 240 km) and wolves (2000–2001: 844 km; 2001–2002: 1077 km; 2002–2003: 865 km) to determine space use and prey use. Wolf movements were snow-tracked for prey kill detection and carcass recovery during continuous intervals lasting an average of 9 d each for a total of 39–61% of the winter period. We tracked cougars specifically when telemetry signals indicated a possible prey kill site in the area (*i.e.*, if an animal was at the same location for at least 2 consecutive days, see Anderson & Lindzey, 2003) or whenever their movements could have brought them near (< 2 km) a wolf pack.

To estimate predator and prey-specific kill rates, we divided the number of kills found by the days monitored. We calculated a kill rate variance for wolves as described in Hebblewhite *et al.* (2003); no kill rate variance was calculated for cougars because monitoring was continuous throughout the winter.

Ground or GPS telemetry, tracks, and distinguishing characteristics of the kill (see O’Gara, 1978; McNay & Voller, 1995) identified predators at kill sites. Concurrently, we identified prey from remains using skull and bone morphology, hair, hooves, and antlers. A chase sequence, blood pool, and/or subcutaneous hemorrhaging distinguished killed prey from prey that died of other causes and was subsequently scavenged. We defined a scavenging event as a wolf or cougar visiting a kill made by a known heterospecific, but we did not include in the present analysis scavenging on animals that died from causes other than predation. We surmised predator displacement from a kill site (usurpation) when a radiocollared individual from one species was localized at a kill site but subsequently left that position when a member of the other species was known to have arrived. Since cougars typically stayed relatively close (< 300 m) to a kill until it was fully consumed (2–10 d), it seems unlikely that a cougar leaving a kill would coincide with the arrival of wolves within the monitoring period unless displacement had occurred. We noted apparent displacement or scavenging by either carnivore on the basis of tracks and other evidence at the kill site.

SPATIAL INTERACTIONS

We used 4 levels of analysis to determine spatial interactions between cougars and wolves. The first level included 2 long-term datasets, one involving monitoring of habitat corridor use by wildlife and the other involving monitoring of animal movements across crossing structures on the Trans-Canada highway. The BNP Wildlife Corridor Project consists of 22 transects established to monitor winter movements of large mammals through wildlife corridors around the town of Banff (Duke, 2001). These transects bisected the

3 major valleys in the area and extended from the boundaries of residential or commercial development to cliff faces or other geographical barriers. We surveyed transects for animal tracks beginning 24 h after each snowfall. During each survey, the numbers and direction of carnivore and ungulate tracks crossing the transect were recorded at 100-m intervals. Snow depth was also recorded. We monitored transects from 1993 to 2004 as snow conditions permitted.

On the highway bisecting the study area, 22 wildlife underpasses and 2 wildlife overpasses provided evidence of crossing structure use by carnivores (Clevenger & Waltho, 2000; Gloyne & Clevenger, 2001). These structures are used extensively by both species when crossing the valley floor, and each structure was equipped with two 2-m tracking pads filled with a dirt and sand substrate suitable for recording track impressions (Clevenger & Waltho, 2000; Gloyne & Clevenger, 2001). We monitored crossing structures every 3–4 d from 1996 to 2004, and the occurrence and number of predators and prey were recorded. We also recorded human use. Both the wildlife corridor and the wildlife crossing structure data sets were based on tracks and therefore did not identify specific individuals or groups.

We used both ground and GPS telemetry to calculate 95% and 50% kernel home ranges (KHR) for each cougar and wolf pack for each of 3 winters, using the Animal Movement extension and default least-squares cross-validation in ArcView (ESRI Inc, Redlands, California, USA; Hooze & Eichenlaub, 1997). We used one location per day (minimum 24 locations, average 83.7 ± 45.9 [SD] locations per individual); when we had more than one location we used the one closest to sunrise. We used KHR to determine the proportion of a cougar’s home range that overlapped with that of a wolf pack (static overlap) and calculated overlap at both home range scales for cougars and wolf packs that exhibited overlap at the 95% KHR. We considered that lack of interspecific overlap at the 95% and 50% KHR was suggestive of strong and weak avoidance of heterospecifics, respectively.

The third level of space use analysis consisted of a dynamic interaction analysis (Kenward, 1992; Poole, 1995) using telemetry locations taken in close temporal sequence for both species. We calculated a mean observed distance between simultaneous locations (defined as < 2 h apart) of paired, sympatric animals and compared this distance with that expected by chance. Averaging distances between each location from one animal and all non-simultaneous locations from the other allowed us to derive expected distances. We used a *t*-test to evaluate differences between observed and expected distances, and classified spatial patterns of cougars, relative to wolves, as avoidance (observed > expected), attraction (observed < expected), or random (observed = expected).

The finest scale of carnivore space-use analysis involved local movement by individuals with respect to heterospecifics. During our snow-tracking sessions we noted when wolf and cougar tracks crossed. Such intersections indicated the temporal sequence of use of shared areas (Paquet, 1991). At these locations, we determined which species made the initial *versus* later track and the age of each track, using telemetry locations and recent snowfall information.

DATA ANALYSIS

We evaluated differences in the proportion of prey species in the diet of cougars and wolves using Chi-square analysis. We also calculated the Renkonen percent diet overlap (Krebs, 1989) between carnivores.

To assess potential temporal avoidance between cougars and wolves, we employed the same analytic approach for wildlife corridors and wildlife crossing structures. First, we restricted our data set only to transects and crossing structures with similar average probabilities (\pm SE) (range 0.05 to 0.4) for either wolf or cougar occurrence during a given monitoring event. This restriction allowed us to avoid possible bias from spatial segregation through differential habitat preference rather than temporal segregation through heterospecific avoidance. Additionally, to maximize independence between track counts on adjacent transects, we selected only those transects that bisected different water-course drainages or were > 5 km apart. Four crossing structures and 9 corridor transects met these criteria.

Next, we modeled cougar occurrence during a monitoring interval using fixed-effects conditional logistic regression (Allison, 1999), stratified by transect and year. Parameters under consideration included the presence of wolves, elk, and alternate prey. Additional variables included snow depth for corridors and human use of the track pads for crossing structures. We first performed a univariate analysis to examine the relationship between independent and dependent variables, and then all relevant combinations of variables were used to create candidate models for the multivariate analysis. Candidate models were evaluated using AIC corrected for small sample sizes (AIC_c ; Anderson, Burnham & Thompson, 2000).

We used 2 different methods to evaluate heterospecific track intersections. First, we tested the sequence of wolf and cougar arrival at a shared location. Based on random walk simulations (A. D. Kortello, unpubl. data), we expected that wolves and cougars moving randomly with respect to one another would have an equal chance of arriving first at a shared location, even if traveling at different speeds. This occurs because the initial location and direction of travel for each animal is indeterminate, as is the intersection point of the 2 paths. Unequal frequencies of first occurrence would be indicative of asymmetrical avoidance (one species tending to move away from the other and occur first) or attraction (one species tending to follow the other and arrive second; see Paquet, 1991). We tested for a random sequence of occurrence by either species using Chi-square analysis; each species had an expected initial occurrence of 50%. We hypothesized that if cougars avoid wolves, more time should elapse between heterospecific track sets if a wolf is there first. Accordingly, we evaluated the timing of track overlap events using a one-tailed *t*-test using the Satterthwaite method for unequal variances, after first normalizing the distributions with a square root transformation. For all statistical tests we considered *P*-values between 0.05 and 0.10 as marginally significant.

Results

In 2000–2001, we radiocollared 8 adult cougars (out of a 2000–2001 population of 8 females, 2 males, and 3 young;

one adult male and one adult female were removed from the population due to human/wildlife conflict incidents at the initiation of the study). In subsequent years, all adults in the population were radiocollared (2001–2002 population: 3 females, 2 males, 3 young; 2002–2003 population: 4 females, 2 males, 4 young). We also monitored 8 wolves (5 females, 3 males) from 2 packs during the study. Populations of large carnivores and their prey underwent notable changes in numbers. The adult cougar population in the study area declined from 10 to 6 animals, while wolf numbers increased from 2 individuals in 1999 to a peak of 15 individuals (in 2 packs) in 2001. In 2003, wolves spent limited time in the study area and numbers declined to about 7–10 individuals (1–2 packs). Throughout 1996–99, elk numbers in the Bow valley were largely stationary at around 600 individuals, but human management led to the relocation of 156 elk (~26%) from the resident population of the study area in 1999–2000, another 35 (~8%) in 2000–2001, and 1 in 2001–2002. Elk numbers continued to decline to about one-third of the original population size during subsequent years (Figure 1). Elk pellet group counts numbered 4580 in 1997, 2146 in 2001, and 2234 in 2003, while alternate prey pellet groups were much less abundant, totalling 715 in 1997, 615 in 2001, and 1362 in 2003.

PREY USE

We located 152 wolf kills during our winter tracking periods. We estimated that wolves killed 88–96 elk during winter 2000–2001 (combined wolf kill rate of 2 packs equalled $0.51 \text{ elk}\cdot\text{d}^{-1}$, 95% C.I. = 0.49–0.53). During 2001–2002, wolves took 41–64 elk (wolf kill rate of $0.29 \text{ elk}\cdot\text{d}^{-1}$, 95% C.I. = 0.23–0.35), whereas in winter 2002–2003 only 5–9 elk were killed (wolf-days in the park were too low to calculate combined kill rates for both packs; however, the kill rate for the Bow Valley pack was $0.014 [0.007\text{--}0.021] \text{ elk}\cdot\text{d}^{-1}$). It follows that the estimated removal rate by wolves was 16–21% of the resident elk population during the first 2 winters of the study, with unknown additional mortality occurring during the summer. In contrast, we located 103 prey killed by cougars during the study, with 3–4 resident animals killing ~17 elk during winter 2000–2001 (cougar kill rate equalled $0.09 \text{ elk}\cdot\text{d}^{-1}$), 8 elk in 2001–2002 ($0.04 \text{ elk}\cdot\text{d}^{-1}$), and 2 elk in 2002–2003 ($0.01 \text{ elk}\cdot\text{d}^{-1}$).

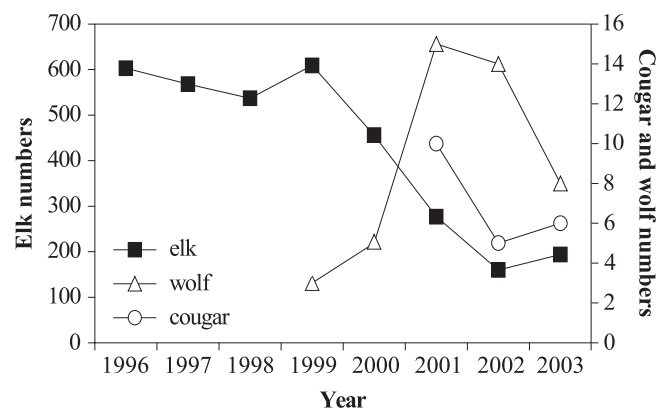


FIGURE 1. Spring population size estimates for elk, wolf, and cougar near Banff, Alberta, 1996–2003.

Accordingly, we estimate that cougars removed between 1% and 4% of the elk population in the Bow Valley each winter. Thus, our results suggest that wolves killed considerably more elk than did cougars throughout the study, but that the impact of wolf predation subsided after 2001–2002.

Cougar kills initially consisted mainly of elk but with time shifted to alternate prey such as deer and bighorn sheep ($\chi^2 = 19.7$, $df = 3$, $P < 0.001$; Figure 2). The use of GPS collars in 2001–2002 and 2002–2003 enabled us to expand our sampling area to more remote portions of cougar home ranges; the observed pattern of prey switching was further substantiated with an additional 2 elk, 8 deer, 19 bighorn sheep, and 1 mountain goat being recovered after 2001 using GPS telemetry.

Wolves also demonstrated a temporal shift in diet, in that they initially relied predominantly on elk but shifted to alternate prey in 2002–2003 ($\chi^2 = 34.6$, $df = 3$, $P < 0.001$; Figure 2). Thus, we observed initial similarity, then divergence, followed by convergence, in the prevalence of elk in the diet of both carnivores (Figure 2). Diet overlap between cougars and wolves was estimated as 90.9% in 1999–2000, 72.6% in 2000–2001, 43.6% in 2001–2002, and 78.9% in 2002–2003.

INTERACTIONS AT KILL SITES

Our telemetry and snowtracking efforts revealed several instances where wolves and cougars interacted at prey kill sites (Table I). In February 2001, wolves killed one radiocollared cougar at its prey kill site. Wolves also displaced cougars directly from their kill sites, as well as scavenged their prey (Table I). Most (83%) instances of wolf scavenging were on elk kills, and cougars rarely (15%, 20 scavenged cougar kills) returned to the kill site after wolves had departed. In contrast, we did not detect any instances where cougars usurped wolf kills ($n = 152$ wolf kills).

SPATIAL INTERACTIONS

Predator track prevalence on corridors and crossing structures suggested a negative relationship between wolf and cougar occurrence. The best multivariate model for predicting cougar presence included variables for both wolf and elk presence (Table II), with each variable having a negative relationship with the probability of finding a cougar track on the transect. The model-averaged odds ratio for cougar tracks occurring when wolf tracks were present was 0.34 (0.18, 0.63; 95% C.I.); the odds ratio for cougar tracks when elk tracks were present was 0.60 (0.42, 0.87).

Patterns of track occurrence at crossing structures were similar to those observed in the corridor analysis. The top ranked multivariate model for species associations at crossing structures included negative relationships between cougar and both wolf and elk (Table II). The model-averaged odds ratio for cougar tracks occurring with wolf tracks was 0.37 (0.15, 0.95); for cougar and elk the odds ratio was 0.78 (0.64, 0.96).

Adjacent cougar and wolf home ranges overlapped an average of $40.4 \pm 6.6\%$ (SE) at the 95% and $19.7 \pm 8.0\%$, at the 50% KHR. Based on our analysis of simultaneous telemetry observations, wolf and cougar spatial proxim-

ity in overlapping home ranges appeared to be random with respect to heterospecifics. Observed simultaneous separation distances did not differ from expected values for all cougar–wolf pack comparisons (range in probability; $P = 0.21$ to 0.99).

Despite this observation, further evidence of spatial displacement was observed at the finest scale of analysis. Analysis of track intersections revealed that the sequence of predator occurrence deviated from random, with cougar tracks being more likely to occur first ($\chi^2 = 7.363$, $df = 1$, $P = 0.007$) (cougars: 30 cases; wolves: 13 cases); this trend was consistent between winters ($\chi^2 = 2.21$, $df = 2$, $P = 0.33$). In addition, the time interval between heterospecific track sets was longer when cougars were the second species present (66.5 ± 22.9 h, $n = 13$ when second; 27.2 ± 4.1 h,

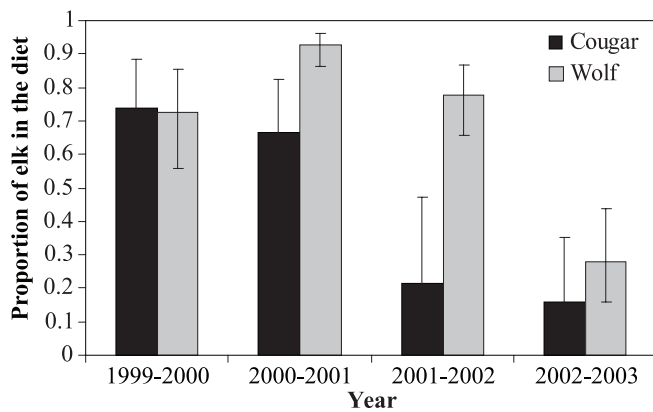


FIGURE 2. Proportion of elk prey in the diet of cougars and wolves as detected by ground telemetry and tracking near Banff, Alberta (1999–2003). Alternative ungulate prey make up the remaining proportion. Error bars are 95% binomial confidence intervals.

TABLE I. Incidences of interference interactions between wolves and cougars near Banff, Alberta (1999–2003).

Year	Percent cougar kills scavenged by wolves	Percent cougar kills usurped by wolves	Percent wolf kills scavenged by cougars
1999–2000	32 (19)	--	5 (22)
2000–2001	33 (21)	10 (21)	6 (67)
2001–2002	29 (14)	14 (14)	7 (45)
2002–2003	16 (19)	11 (19)	0 (18)

Note: Sample size is in parentheses.

TABLE II. Logistic regression models of species associations predicting cougar presence in wildlife corridors (1993–2003) and wildlife crossing structures (1996–2003) near Banff, Alberta.

Source	Odds Ratio	95% C.I. (wolf)	95% C.I. (elk)	ΔAIC_c	w_i
Corridor	0.34(wolf) + 0.57(elk)	0.64, 0.47	0.88, 0.37	0	0.896
Corridor	0.37(wolf)	0.69, 0.20	--	4.373	0.100
Corridor	0.63(elk)	--	0.97, 0.41	10.891	0.004
Structure	0.32(wolf) + 0.69(elk)	1.06, 0.10	1.08, 0.44	0	0.518
Structure	0.32(wolf)	1.05, 0.10	--	0.769	0.352
Structure	0.68(elk)	--	1.07, 0.44	2.762	0.130

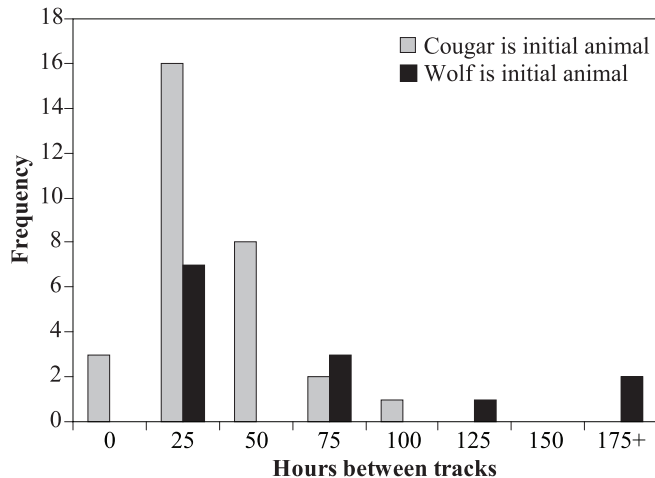


FIGURE 3. Time elapsed since heterospecific use of shared locations for wolves and cougars as determined by track intersections, near Banff, Alberta (2001–2003).

$n = 30$ when first, $df_{adj} = 14.7$, $t = -1.7$, $P_{one\ tailed} = 0.055$; Figure 3), which further implies wolf avoidance by cougars.

Discussion

Behavioural mechanisms promoting coexistence between sympatric species sharing resources include direct avoidance and/or resource partitioning. If the outcome of competitive interactions is asymmetric, then spatial displacement or niche shifts will occur in the losing species (Petren & Case, 1996; Holmgren, 1995); this prediction is consistent with observations in the present study. Wolf- and human-mediated decline in elk numbers in the study area was associated with cougar diet shift from primarily elk to mainly deer and bighorn sheep. Cougars also showed avoidance of areas used by wolves (at most but not all scales of analysis) and non-random use of shared space. Although wolves also exhibited diet shift that coincided with the observed elk decline, this shift lagged behind that of cougars by 1 y and was also associated with a marked decrease in wolf use of the study area.

Exploitative interactions are indirect and mediated through responses to shared food or space resources (Petren & Case, 1996). Niche shift is one outcome of increasing exploitative competition, such that demonstrating that one species negatively affects resource use by another is a central factor in demonstrating exploitation (Petren & Case, 1996). In our study, elk initially made up most of both cougar and wolf diets in the study area (Paquet, 1993; Hebblewhite, Pletscher & Paquet, 2002). However, the low cougar numbers and kill rates observed in the study area contributed to a minor demographic impact of cougars on the elk population (see also McKenzie, 2001). In contrast, Hebblewhite, Pletscher, and Paquet (2002) demonstrated that winter wolf predation was demographically significant to elk populations in BNP. Hence, the observed diet switch by cougars from elk to alternative prey during a period of increasing wolf and decreasing elk populations is suggestive of exploitative competition between the 2 predators. It is

unlikely that an increase in deer and bighorn sheep numbers was responsible because in 2001, the year of the cougar diet switch, pellet group counts for alternative prey were at their lowest. We also discount the possibility that the decline in elk numbers was solely human-mediated because substantial human impacts to the elk population occurred only in 1999–2000. In subsequent years, wolf predation accounted for much higher losses to the elk population than management actions, and the elk population did not stabilize until both wolf packs had largely migrated out of the study area. This implies that high wolf predation rates were importantly involved in the elk decline.

The diet shift of wolves in response to the elk decline was delayed relative to that of cougars, suggesting that predation rates were compensatory for a short period and thus further depressed prey populations; this trait tends to be characteristic of the stronger competitor species (Holt, Grover & Tilman, 1994). Whereas previous studies also have shown high diet overlap between wolves and cougars (Kunkel *et al.*, 1999; Husseman *et al.*, 2003), ours is the first to report dramatic and sequential prey shifts in both predator species. This pattern of diet change is expected among coexisting species that follow the sequence of *i*) responding opportunistically to superabundant food resources, *ii*) specializing as food resources become more limiting, and then *iii*) converging on alternate prey as food becomes more scarce (*e.g.*, see Wiens, 1993).

Interference competition is arguably more important (or at least more easily detected) than is exploitative competition (Schoener, 1982). Evidence for interference competition in our study includes wolves usurping prey kills from cougars and killing a cougar. In theory, even simple behaviours, such as avoidance, can reduce competitive effects by weakening density-dependent relationships between sympatric and potentially competing species (Mitchell *et al.*, 1990; Chesson & Rosenzweig, 1991). Hence, interference should influence the distribution of foraging animals (Parker & Sutherland, 1986; Holmgren, 1995). We predicted that cougars would mitigate direct interference by avoiding wolves in space or time, which was borne out in analyses at multiple spatial and temporal scales.

Overall, wolf and cougar home ranges showed considerable overlap and thus no direct evidence of competitive avoidance. However, at a smaller spatial and temporal scale, the negative relationship between cougar and wolf space use was discernable in both crossing structure and wildlife corridor analyses. The weaker negative relationship between cougars and elk in corridor and crossing structure models is probably due to predator avoidance behaviour on the part of elk (Creel *et al.*, 2005; Fortin *et al.*, 2005). Irrespective of the absence of a cause and effect relationship in these data, it is evident that spatial avoidance did exist between cougars and wolves. Similarly, at the finest scale, interspecific track intersections showed evidence of cougar avoidance of wolves, either by rarely arriving second at a given location or by allowing more time to elapse before using locations where wolves were recently present. Thus, it seems clear that wolves were the dominant competitor and that cougars responded behaviourally to wolf presence. Although we failed to observe clear signs of cougar

avoidance of wolves in the dynamic interaction analysis, in retrospect it seems likely that in the heavily forested terrain of BNP the detection and avoidance of wolves by cougars might have occurred at shorter distances than those that could be observed by telemetry (see also White, Ralls & Garrott, 1994).

The small populations of carnivores in this study are subject to stochastic changes affecting population size, demographics, and sex ratios, and these can have possible behavioural consequences. This limits the power of our inference. However, although we did not obtain specific information on age and gender from track data sets, wolf pack sizes ranging from 1 to 17 and males, females, and family groups of cougars were tracked in corridors and on wildlife crossing structures. We feel that, given this observed variability, the long-term nature of the data on spatial interactions between wolves and cougars indicate that avoidance is the general response. Predation in cougars may be size or sex biased, with larger males tending to kill larger prey (Murphy, 1998). However, female cougars appeared quite capable of killing elk, and there is no indication here that the switch to smaller alternative prey was due to a higher proportion of females in the population—the opposite was true. For wolves, populations appeared more affected by dispersal than demographic processes, and changes in predation appeared consistent irrespective of pack structure.

There is growing awareness of the importance of intra-guild interactions in the distribution, abundance, and population dynamics of carnivores and their effect on prey populations (Holt & Polis, 1997; Palomares & Caro, 1999; Linnell & Strand, 2000). This study reveals that wolf recolonization can affect cougar prey and space use patterns. Since cougars have co-evolved and co-existed with wolves, these methods of resource partitioning, in combination with other behaviours such as a preference for steeper terrain, caching prey to minimize usurpation, and the ability to escape direct conflict by climbing trees, may contribute to cougar persistence in areas of sympatry (Duke, 2001; Ruth, 2004). However, the long-term effects of wolves on cougar population demographics and carrying capacity are not well understood and may have been important historically in determining ecosystem function and processes. For example, using archival data on bounty harvest records, Riley, Nesslage, and Maurer (2004) found an inverse spatial pattern of abundance for wolves and cougars in Montana. It is also interesting to note that the BNP cougar population experienced low annual survival rates during wolf recolonization (annual rate: 0.513; 0.301–0.875; $n = 6$ deaths, see Heisey & Fuller, 1985; the calculated rate is for radio-collared animals only and does not include the population losses due to management actions at the commencement of the study). Although only one mortality was directly attributable to wolves, food limitation resulting from the decline in prey abundance may have contributed to the high mortality rates. Indeed, most cougar carcasses that we recovered were thin or emaciated. In contrast, although the annual survival rate for wolves was similarly low during the study (annual rate: 0.510; 0.290–0.870, $n = 6$ deaths), all wolf mortalities were directly due to humans, and recovered carcasses were generally in good condition (A. D. Kortello, unpubl.

data). This suggests a possible population response to interactions, although cougars certainly did not vanish from the area.

While the high mountain ranges and narrow valleys occurring in our study area may have restricted movements and dispersal and thereby accentuated agonistic and exploitative interactions between predators (Gurevitch *et al.*, 1992), the responses that we observed in BNP are potentially representative of other cases where wolves are recolonizing areas across western North America. Clearly, future research efforts need to further elucidate population-level responses of resident carnivores following wolf population expansion and increase, and these relationships should be used to develop conservation and management strategies that will ensure persistence of both recolonizing wolves and resident species.

Acknowledgements

Funding for this research came from Parks Canada. We thank J. Jorgenson of Alberta Sustainable Resource Development, C. Callaghan of the Central Rockies Wolf Project, T. Clevenger of the Trans-Canada Highway Project, and the Banff Corridor Wolf and Elk Projects for data sharing and collaboration. Banff Park warden T. Davidson was crucial for his involvement and support with all aspects of this project. Invaluable field assistance was provided by S. Ham, E. Knight, D. Thompson, A. Domes, and numerous other technicians and volunteers.

Literature cited

- Allison, P. D., 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute Inc., Cary, North Carolina.
- Anderson, D. R., K. P. Burnham & W. L. Thompson, 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management*, 64: 912–923.
- Anderson, C. R., Jr. & F. G. Lindzey, 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management*, 67: 307–316.
- Arjo, W. M. & D. H. Pletscher, 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Canadian Journal of Zoology*, 77: 1919–1927.
- Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack & C. C. Niemeyer, 1998. Status of grey wolf restoration in Montana, Idaho, and Wyoming. *Wildlife Society Bulletin*, 26: 785–798.
- Boyd, D. K. & G. K. Neale, 1992. An adult cougar, *Felis concolor*, killed by gray wolves, *Canis lupus*, in Glacier National Park, Montana. *Canadian Field-Naturalist*, 106: 524–525.
- Chesson, P. & M. Rosenzweig, 1991. Behavior, heterogeneity and the dynamics of interacting species. *Ecology*, 72: 1187–1195.
- Clevenger, A. P. & N. Waltho, 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology*, 14: 47–56.
- Creel, S. & N. M. Creel, 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, 10: 526–538.
- Creel, S., J. Winnie Jr., B. Maxwell, K. Hamlin & M. Creel, 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86: 3387–3397.
- Duke, D., 2001. Wildlife Use of Corridors in the Central Canadian Rockies: Multivariate Use of Habitat Characteristics and Trends in Corridor Use. M.Sc. thesis, University of Alberta, Edmonton, Alberta.

- Durant, S. M., 1998. Competition refuges and coexistence: An example from Serengeti carnivores. *Journal of Animal Ecology*, 67: 370–386.
- Elmhagen, B., M. Tannerfeldt & A. Angerbjörn, 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology*, 80: 1274–1285.
- Fedriani, J. M., F. Palomares & M. Delibes, 1999. Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, 121: 138–148.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne & J. S. Mao, 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86: 1320–1330.
- Gloyne, C. C. & A. P. Clevenger, 2001. Cougar use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. *Wildlife Biology*, 7: 117–124.
- Gurevitch, J., L. L. Morrow, A. Wallace & J. S. Walsh, 1992. A meta-analysis of field experiments on competition. *American Naturalist*, 140: 539–572.
- Hebblewhite, M., 2000. Wolf and Elk Predator–Prey Dynamics in Banff National Park. M.Sc. thesis, University of Montana, Missoula, Montana.
- Hebblewhite, M., D. H. Pletscher & P. C. Paquet, 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, 80: 789–799.
- Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard & C. J. Callaghan, 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. *Wildlife Society Bulletin*, 31: 933–946.
- Heisey, D. M. & T. K. Fuller, 1985. Evaluation of survival and cause-specific mortality rates using telemetry. *Journal of Wildlife Management*, 49: 668–674.
- Holland, W. D. & G. M. Coen, 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume II. Soil and vegetation resources. Publ. No. SS-82-44, Alberta Institute of Pedology, Edmonton, Alberta.
- Holmgren, N., 1995. The ideal free distribution of unequal competitors: Predictions from a behavior-based functional response. *Journal of Animal Ecology*, 64: 197–212.
- Holroyd, G. L. & K. J. Van Tighem (eds.), 1983. Ecological (Biophysical) Land classification of Banff and Jasper National Parks. Volume I. The wildlife inventory. Part A. Canadian Wildlife Service, Edmonton, Alberta.
- Holt, R. D. & G. A. Polis, 1997. A theoretical framework for intra-guild predation. *American Naturalist*, 149: 745–764.
- Holt, R. D., J. Grover & D. Tilman, 1994. Simple rules for interspecific dominance in systems with exploitative and interference competition. *American Naturalist*, 144: 741–771.
- Hooge, P. N. & B. Eichenlaub, 1997. Animal movement extension to Arcview version 1.1. Alaska Biological Science Center, US Geological Survey, Anchorage, Alaska.
- Huggard, D. J., 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology*, 71: 130–139.
- Hussemann, J., D. L. Murray, G. Power, C. Mack, C. R. Wenger & H. Quigley, 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, 101: 591–601.
- Jacobson, P. & R. Kunelius, 1985. Banff Wildlife Monitoring Plan. Appendix IV: Methodology for Bow Valley Aerial Elk Surveys, Banff National Park. Banff Warden Service, Parks Canada, Banff, Alberta.
- Kenward, R. E., 1992. Quantity versus quality: Programmed collection and analysis of radio-tracking data. Pages 231–246 in S. M. Smith (ed.). *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ellis Horwood, Chichester.
- Krebs, C. J., 1989. *Ecological Methodology*. Harper-Collins Publishers, New York, New York.
- Kreeger, T. J., 1999. *Handbook of Wildlife Chemical Immobilization*. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado.
- Kunkel, K. E. & D. H. Pletscher, 1999. Species-specific population dynamics of cervids in a multipredator ecosystem. *Journal of Wildlife Management*, 63: 1082–1093.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher & M. G. Hornocker, 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management*, 63: 901–910.
- Linnell, J. D. C. & O. Strand, 2000. Interference interactions, coexistence and conservation of mammalian carnivores. *Diversity and Distributions*, 6: 169–176.
- Litvaitis, J. A. & D. J. Harrison, 1989. Bobcat–coyote niche relationships during a period of coyote population increase. *Canadian Journal of Zoology*, 67: 1180–1188.
- McKenzie, J., 2001. The Selective Advantage of Urban Habitat Use by Elk in Banff National Park. M.Sc. thesis, University of Guelph, Guelph, Ontario.
- McNay, R. S. & J. M. Voller, 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. *Journal of Wildlife Management*, 59: 138–146.
- Mitchell, W. A., Z. Abramsky, B. P. Kotler, B. Pinshow & J. S. Brown, 1990. The effect of competition on foraging activity in desert rodents: Theory and experiments. *Ecology*, 71: 844–854.
- Murphy, K. M., 1998. The Ecology of the Cougar (*Puma concolor*) in the Northern Yellowstone Ecosystem: Interactions with Prey, Bears, and Humans. Ph.D. thesis, University of Idaho, Moscow, Idaho.
- Nowak, R. M., 1999. *Walker's Mammals of the World*. 6th Edition. The Johns Hopkins University Press, Baltimore and London.
- O’Gara, B., 1978. Differential characteristics of predator kills. *Proceedings of the Biennial Pronghorn Antelope Workshop*, 8: 380–393.
- Palomares, F. & T. M. Caro, 1999. Interspecific killing among mammalian carnivores. *American Naturalist*, 153: 492–508.
- Paquet, P. C., 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy*, 72: 397–401.
- Paquet, P. C., 1993. Summary reference document: Ecological studies of recolonizing wolves in the central Canadian rocky mountains. Final Report. Parks Canada, Banff National Park, Banff, Alberta.
- Paquet, P. C., J. Wierzchowski & C. Callaghan, 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in J. Green, C. Pacas, S. Bayley & L. Cornwell (eds.). *A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley*. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ontario.
- Parker, G. A. & W. J. Sutherland, 1986. Ideal free distribution when individuals differ in competitive ability: Phenotype limited ideal free models. *Animal Behaviour*, 34: 1222–1242.
- Petren, K. & T. Case, 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology*, 77: 118–132.
- Poole, K., 1995. Spatial organization of a lynx population. *Canadian Journal of Zoology*, 73: 632–641.

- Riley, S. J., G. M. Nesslage & B. A. Maurer, 2004. Dynamics of early wolf and cougar eradication efforts in Montana: Implications for conservation. *Biological Conservation*, 119: 575–579.
- Ruth, T. S., 2004. Patterns of Resource Use among Cougars and Wolves in Northwestern Montana and Southeastern British Columbia. Ph.D. thesis, University of Idaho, Moscow, Idaho.
- Sinclair, A. R. E., 1991. Science and the practice of wildlife management. *Journal of Wildlife Management*, 55: 767–773.
- Schoener, T. W., 1982. The controversy over interspecific competition. *American Scientist*, 70: 586–595.
- Thornton, D. H., M. E. Sunquist & M. B. Main, 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. *Journal of Mammalogy*, 85: 973–982.
- Wiens, J. A., 1993. Fat times, lean times and competition among predators. *Trends in Ecology and Evolution*, 8: 348–349.
- Witmer, G. W. & D. S. deCalesta, 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. *Canadian Journal of Zoology*, 64: 2333–2338.
- White, P. J., K. Ralls & R. A. Garrot, 1994. Coyote–kit fox interactions as revealed by telemetry. *Canadian Journal of Zoology*, 72: 1831–1836.