Interference competition between gray wolves and coyotes in Yellowstone National Park

J.A. Merkle, D.R. Stahler, and D.W. Smith

Abstract: Factors influencing the outcome of interspecific interactions between sympatric carnivores, along with population-level consequences, are not clearly understood. The reintroduction of gray wolves (*Canis lupus* L., 1758) to Yellowstone National Park provides a rare opportunity to study interactions with coyotes (*Canis latrans* Say, 1823), which had lived in the absence of wolves for >60 years. We evaluated direct interactions between wolves and coyotes to identify factors influencing the outcomes of interspecific interactions and describe the context and degree of competition and coexistence. Using radio-collared wolves, we documented 337 wolf–coyote interactions from 1995 to 2007. The majority (75%) of interactions occurred at ungulate-carcass sites. Wolves initiated the majority of encounters (85%), generally outnumbered coyotes (39%), and dominated (91%) most interactions. Wolves typically (79%) chased coyotes without physical contact; however, 25 interactions (7%) resulted in a coyote death. Interactions decreased over time, suggesting coyote adaptation or a decline in coyote density. In the majority (80%) of fatal interactions, wolves outnumbered coyotes. However, wolves did not outnumber coyotes in interactions (*n* = 18) where coyotes chased or attacked/harassed wolves. Our results suggest that wolves are the dominant canid, group size may influence the outcome of interactions, and coyotes must benefit from the access to carrion at wolf-killed carcasses.

Résumé : On ne comprend pas clairement les facteurs qui influencent l'issue des interactions interspécifiques entre les carnivores sympatriques, ni les conséquences de ces interactions à l'échelle démographique. La réintroduction des loups communs (*Canis lupus* L., 1758) dans le parc national de Yellowstone fournit une occasion unique d'étudier leurs interactions avec les coyotes (*Canis latrans* Say, 1823) qui ont vécu en l'absence de loups pendant >60 ans. Nous avons évalué les interactions directes entre les loups et les coyotes afin d'identifier les facteurs qui influencent les issues de ces interactions interspécifiques et de décrire le contexte et l'importance de la compétition et de la coexistence. L'utilisation de loups munis de colliers radio nous a permis de consigner des informations sur 337 interactions loups–coyotes de 1995 à 2007. La majorité (75 %) des interactions ont eu lieu près de carcasses d'ongulés. Les loups ont entamé la majorité des rencontres (85 %), ils surpassaient généralement les coyotes en nombre (39 %) et ils dominaient la plupart des interactions (91 %). De façon habituelle (79 %), les loups chassaient les coyotes, sans établir de contact physique; cependant, 25 interactions (7 %) ont entraîné la mort d'un coyote. Les interactions sont devenues moins nombreuses avec le temps, ce qui laisse croire à une adaptation ou un déclin de la densité chez les coyotes. Dans la majorité des interactions fatales (80 %), les loups étaient plus nombreux que les coyotes. Cependant, les loups ne surpassaient pas en nombre les coyotes dans les interactions (*n* = 18) dans lesquelles les coyotes ont chassé ou attaqué/harcelé les loups. Nos résultats laissent penser que les loups sont les canidés dominants, que la taille des groupes peut influencer l'issue des interactions et que les coyotes doivent tirer un certain bénéfice de leur accès à la charogne des carcasses tuées par les loups.

[Traduit par la Rédaction]

Introduction

Interspecific competition between predators can be a driving force in community ecology (Schoener 1983). Consequently, advancing our understanding of intraguild interactions is not only important for the conservation success of species like large carnivores (Creel et al. 2001), but can play a critical role in linking this aspect of food-web dynamics to ecosystem-level processes and management (Estes 1996). With the restoration of predators to ecosystems, broad-scaled analyses of direct and indirect species inter-

actions are underway, with emphasis on top-down effects of carnivores on multiple trophic levels (Schmitz et al. 2000; Berger et al. 2001; Terborgh et al. 2001; Hebblewhite et al. 2005). Less emphasized are studies on the influence of top predators on other predator populations (Linnell and Strand 2000), even though these interactions may be important (Rosenzweig 1966; Case and Gilpin 1974).

Interspecific interactions played a role in the evolution of sympatric predators (Van Valkenburgh 1991) and have important implications for the structure and function of carnivore communities (Palomares and Caro 1999; Caro and Stoner 2003). Direct and indirect forms of competition can occur between carnivore species. Exploitative competition occurs through indirect interaction when a species out competes another for a common resource (Case and Gilpin 1974). Interference competition is a direct interaction involving harassment, kleptoparasitism, or outright killing (Linnell and Strand 2000). Collectively, both forms of competition influence ecological functions, food-web dynamics

J.A. Merkle, D.R. Stahler,[1] and D.W. Smith. Yellowstone Wolf Project, Yellowstone Center for Resources, Wolf Project, P.O. Box 168, Yellowstone National Park, WY 82190, USA.

[1]Corresponding author (e-mail: dan_stahler@nps.gov).

(Case and Gilpin 1974; Finke and Denno 2005; Byrnes et al. 2006), and the distribution and density of predator populations (Polis and Holt 1992; Palomares and Caro 1999; Creel et al. 2001; Smallegange et al. 2006).

In North American ecosystems where gray wolves (*Canis lupus* L., 1758) occur, interactions with other members of the carnivore guild are common, with competition presumably being most intense with species of similar ecology (Palomares and Caro 1999; Ballard et al. 2003) and size (Rosenzweig 1966). Interference competition among wolves and coyotes (*Canis latrans* Say, 1823) can influence the abundance and distribution of coyotes (Thurber et al. 1992; Peterson 1995; Berger and Gese 2007), with densities of both species often inversely related (Berg and Chesness 1978; Paquet 1991; Thurber et al. 1992; Peterson 1995). With wolves being the behaviorally dominant carnivore, coyotes can avoid interactions by temporal separation (Carbyn 1982; Arjo and Pletscher 1999), spatial avoidance (Berg and Chesness 1978; Fuller and Keith 1981; Dekker 1989; Paquet 1992; Thurber et al. 1992), and alternate diets (Thurber et al. 1992). However, the diets of sympatric wolves and coyotes overlap (Paquet 1992), and competition for resources is common. Specifically, wolf-killed ungulate carcasses can provide significant food for scavenger species such as coyotes, and in effect enhance and concentrate interspecific interactions (Ballard et al. 2003; Wilmers et al. 2003).

Historically, coyotes and wolves coexisted in Yellowstone National Park (YNP; Murie 1940; Schullery and Whittlesey 1992). However, federal control programs led to the demise of wolves in YNP by 1930 (Bangs and Fritts 1996). Coyotes persisted in the absence of wolves for >60 years (U.S. Fish and Wildlife Service 1994) despite similar persecution, and occurred at high densities in the absence of wolves (Gese et al. 1996*a*, 1996*b*). In 1995 and 1996, wolves were reintroduced into YNP, and the population increased to 174 in 2003 (Smith et al. 2004*a*). Since then, the wolf population has stabilized between 118 and 169 individuals. Since wolf reintroduction, coyotes are still the most abundant carnivore (N = 800–1000; Gunther et al. 2000), but competition with wolves seems to influence their density (Berger and Gese 2007). For example, coyote densities in the Lamar River Valley of northeastern YNP declined 39% following wolf reintroduction (Berger and Gese 2007); the decline was 50% in the 3 years after reintroduction in 1995 (Crabtree and Sheldon 1999).

Although reports of wolf–coyote interactions and wolf-caused coyote mortality are common (Ballard et al. 2003), the factors influencing the outcome of interspecific interactions, as well as population-level consequences, are not clearly understood (but see Berger and Gese 2007). This is presumably due to the elusive nature of these carnivores and that relatively few areas contain both sympatrically, making documentation of interactions between coyotes and wolves difficult.

As part of our effort to evaluate the effects of wolf recovery on sympatric carnivore communities and food-web dynamics in YNP, we monitored interactions between wolves and coyotes over 12 years following reintroduction. Our objective was to describe the context and degree of interaction between the two canids to test several predictions regarding intraguild competition. First, because wolves are bigger and typically associate in larger groups, we predicted that wolves would dominate interactions and occasionally kill coyotes. Second, owing to overlapping diets of carrion, we predicted that most interactions would occur at wolf-killed ungulate carcasses where competition would be greatest because wolves defend their food. Third, we expected group size to influence interaction outcomes, specifically benefiting coyotes during interactions where their group size was greater. Fourth, we predicted that the frequency of wolf–coyote interactions would be (*i*) greater during the early years of wolf recolonization, as coyotes would be relatively naïve to a dominant competitor, and (*ii*) positively correlated with wolf density. In addition, we consider our results on the type and frequency of interactions in reference to the potential or limiting mechanisms for wolf–coyote hybridization to occur. Understanding the factors that influence interactions between wolves and coyotes will help elucidate the mechanisms underlying interference competition and selection for adaptive behavior under sympatry.

Materials and methods

Study area

We conducted fieldwork in YNP from 1995 to 2007. Yellowstone National Park is an 8991 km² area primarily in northwestern Wyoming that is protected from hunting, livestock grazing, and resource development. The study area contains variable elevation (1500–3300 m), precipitation (26–205 cm), temperature (–40 to 30 °C), soil, vegetation, and topography, providing a variety of habitats from high alpine to sagebrush grasslands (Haines 1977; Despain 1990). Most observations of wolves (>99%) occurred in a 995 km² area in the northern quarter of YNP, known as the Northern Range (NR). The NR supports the largest migrating elk (*Cervus elaphus* L., 1758) herd in YNP (Singer and Mack 1993), numbering between 6 738 and 14 538 (minimum counts, not adjusted for sightability) elk during the study. As a result, the highest wolf densities in YNP are found on the NR. Most of the NR is steppe to shrub–steppe (55%) dominated by Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), and big sagebrush (*Artemisia tridentata* Nutt.). Conifer forest with small amounts of quaking aspen (*Populus tremuloides* Michx.) and willow (genus *Salix* L.) cover 41% of the NR (Coughenour and Singer 1996). This primarily open area, bisected by a road that is accessible all year, provided a unique opportunity to observe wolf interactions from the ground.

Most flora and fauna documented when YNP was established are present today, including all large ungulates and carnivores (Schullery 1996; Pritchard 1999; Morrison et al. 2007). The main carnivores include wolves, coyotes, mountain lions (*Puma concolor* (L., 1771)), grizzly bears (*Ursus arctos* L., 1758), and black bears (*Ursus americanus* Pallas, 1780). Ungulates occupying YNP include elk, bison (*Bison bison* (L., 1758)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), and to a lesser extent, moose (*Alces alces* (L., 1758)), pronghorn (*Antilocapra americana* (Ord, 1815)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), bighorn sheep (*Ovis canadensis* Shaw, 1804), and mountain goats (*Oreamnos americanus* (de Blainville, 1816)) (Singer and Mack 1993; Bangs and Fritts 1996).

Field observations

Thirty-one gray wolves were captured in Canada, radio-marked, and reintroduced into various areas of YNP in 1995 and 1996 (Bangs and Fritts 1996; Fritts et al. 1997). Following reintroduction, approximately 20–30 wolves were radio-collared annually, resulting in 30%–40% of the population marked and a minimum of one radio collar in each study pack (Smith et al. 2004b). During collaring, wolves were handled in accordance with the *Guide to the Care and Use of Experimental Animals* (Canadian Council of Animal Care 1984), and National Park Service guidelines. From 1995 to 2007, the known wolf population ranged between 14 and 174 wolves composing 2–13 packs, with 2–37 individuals per pack. Exact coyote numbers were not known; however, population estimates immediately following wolf reintroduction were 800–1000 coyotes in YNP (Gunther et al. 2000). We recorded behavioral interactions between wolves and coyotes primarily during biannual predation studies designed to determine predation rates and prey selection in early (15 November – 14 December) and late winter (1–30 March; Smith et al. 2004b). Interspecific interactions were also recorded opportunistically outside of these study periods. Direct open-field observations were made from distances of 0.15–4.0 km of radio-collared and unmarked wolves facilitated by radiotelemetry, known territory-use patterns, and 25×–60× spotting scopes. For many of the wolf packs observed, age, sex, and social status (breeder or nonbreeder) of pack members were known through handling and field observations. Similar information for coyotes was unknown. Upon visual detection of wolves and coyotes within the same field of view showing obvious recognition of the other's presence, we began an all-occurrence sampling period (Altmann 1974) for the duration of the interaction.

As the two species began direct behavioral interaction, we recorded (*i*) duration of interaction, (*ii*) site characteristic, (*iii*) number of wolves and coyotes present (the number of individuals within a given area in which direct behavioral interaction can occur) and (or) involved (the number of individuals within a given area that performed a behavior directed towards the other species), (*iv*) age and social status of wolves involved if known, (*v*) which species initiated the interactions (the species that first engaged in a behavior directed at the opposite species), (*vi*) interaction type, and (*vii*) which species dominated the interactions (a species dominates when the other leaves the immediate area or kills the other species). Site characteristics at which an interaction took place were classified as either (*i*) ungulate carcass, (*ii*) active coyote den, (*iii*) active wolf den, or (*iv*) neutral site (defined as a site on the landscape void of the three aforementioned characteristics). The age and social status of wolves involved were classified as (*i*) pup, (*ii*) nonbreeding adult, (*iii*) breeding adult, and (*iv*) unknown. We classified interaction type based on the following defined outcomes — (*i*) neutral: wolf and coyote ignore each other and (or) display no aggressive behavior; (*ii*) wolf chases coyote: wolf runs towards coyote and the latter flees with no physical contact; (*iii*) wolf attacks/harasses coyote: wolf physically contacts, bites, or restrains, but does not kill coyote; (*iv*) wolf kills coyote; (*v*) coyote chases wolf: coyote runs towards wolf and the latter flees with no physical contact;

and (*vi*) coyote attacks/harasses wolf: coyote physically contacts, bites, or restrains, but does not kill wolf.

Analysis

We used two-sample *t* tests to compare means between numbers of wolves and coyotes involved and present during interactions (Ott and Longnecker 2001). Not all data met normality and equal variance assumptions (quantile–quantile plots not shown); however, all contained large samples and nonparametric tests (i.e., Wilcoxon rank sum tests) provided similar results (Ott and Longnecker 2001). To test for patterns of interference competition that may result from seasonal differences in carrion abundance, we compared coyote mortality rates between early winter (when prey are presumably less physiologically stressed) and late winter (when prey are more vulnerable and wolf kill rates are higher; Smith et al. 2004b) using a Fisher's exact test (Zar 1999). To measure the variation in wolf–coyote interactions and wolf densities over time, we analyzed R^2 values from fitted nonlinear regression equations. A variety of functions were assessed using a curve estimation procedure. We considered second- and third-order polynomials in both instances, but we chose regression models with the best fit while maximizing our degrees of freedom. All analyses were conducted with SPSS® for Windows® version 14.0 (SPSS Inc. 2005), using a significance value of 0.05.

Results

We observed 337 wolf–coyote interactions between 1995 and 2007 in YNP involving 15 different wolf packs. The majority of interactions (99%) were observed on the NR, with 78% (*n* = 263) of them recorded during the biannual 30-day winter study periods. On average, the duration of interactions was 6.55 ± 1.0 min (range 1–105 min).

Interactions where wolves chased coyotes (79% of interactions) were most common. Other interactions ranged from wolves killing coyotes (7%) to coyotes attacking/harassing wolves (1%; Table 1). The majority (75%) of wolf–coyote interactions took place at ungulate carcasses, whereas other interactions occurred at neutral sites (20%), active wolf dens (2%), and active coyote dens (2%; Table 1). On average, 3.15 ± 0.17 wolves (range 1–15 wolves) and 2.20 ± 0.09 coyotes (range 1–13 coyotes) were involved in interactions. Approximately half (*n* = 151) of the interactions involved a single wolf (Table 2). In most observed interactions, wolves outnumbered coyotes (44%) and were the initiator (85%). Wolves (91%) mostly dominated interactions, whereas coyote (6%) and no domination (3%) were rarely documented (Table 1). Coyotes never dominated interactions when >2 wolves were involved in the interaction (Table 2). The age-class breakdown of wolves involved in interactions was 25% pups, 22% breeding adults, 22% nonbreeding adults, and 31% unknown age wolves, but varied by the number of wolves involved (Table 2).

Twenty-five (7%) wolf–coyote interactions resulted in the death of a coyote (Table 1). However, during winter studies, where effort was consistent and all interactions were recorded, 10 of 263 (4%) interactions resulted in death of the coyote. We observed seven and three interactions resulting in a coyote death during early-winter and late-winter studies,

Table 1. Gray wolf (*Canis lupus*) and coyote (*Canis latrans*) interactions in Yellowstone National Park, Wyoming, 1995–2007.

	Interaction type							
	Neutral	Wolf chases coyote	Wolf attacks/ harasses coyote	Wolf kills coyote	Coyote chases wolf	Coyote attacks/harasses wolf	Total	Percentage
No. of occurrences	19	267	8	25	14	4	337	
Percentage of occurrences	6	79	2	7	4	1		
Type of site								
Carcass	10	218	6	16	4	0	254	75
Coyote den	0	3	1	3	1	0	8	2
Wolf den	0	5	0	1	0	0	6	2
Neutral	9	41	1	5	9	4	69	20
Initiation								
Wolf	9	246	7	23	0	0	285	85
Coyote	10	13	0	0	13	4	40	12
Unknown	0	8	1	2	1	0	12	4
No. of each								
Coyotes > wolves	6	54	2	1	12	3	78	23
Wolves > coyotes	7	120	2	20	0	0	149	44
Coyotes = wolves	6	93	4	4	2	1	110	33
Outcome								
Wolf dominates	7	267	8	25	0	0	307	91
Coyote dominates	1	0	0	0	14	4	19	6
No domination	11	0	0	0	0	0	11	3

respectively. However, the mortality rate resulting from interactions was not significantly higher during early winter (6.4%) than late winter (1.9%; Fisher's exact test, $P = 0.098$). Additionally, mortality rates varied with respect to the number of wolves involved in interactions (Table 2). We were not able to compare mortality rates annually because of small sample sizes.

The number of wolves involved in interactions did not always equal the number of wolves present (Table 3). The number of wolves and coyotes present and involved varied between interactions where wolves killed coyotes and interactions when they did not (Table 3). The total number of wolves present was not significantly different ($t_{[335]} = 1.22$, $P = 0.11$) between nonfatal and fatal interactions, but more wolves were involved in fatal interactions ($t_{[335]} = 5.33$, $P < 0.0001$; Table 3). The number of coyotes involved or present was not different between fatal and nonfatal interactions ($t_{[335]} = -1.15$, $P = 0.12$; $t_{[335]} = -1.42$, $P = 0.079$, respectively). However, during interactions where coyotes dominated ($n = 19$), more coyotes were involved (2.42 ± 0.2) than not involved (1.67 ± 0.1) ($t_{[335]} = 2.66$, $P = 0.004$).

To evaluate whether a temporal pattern in the frequency of wolf and coyote interactions occurred over the study period, we used interactions recorded during winter study periods from 1997 to 2007, adjusted for effort (no. of interactions per minute that wolves were in view). We omitted interactions from 1995 and 1996 because we were not systematically documenting interspecific interactions. The number of wolf and coyote interactions decreased ($R^2 = 0.775$, $F_{[2,7]} = 12.033$, $P = 0.005$; Fig. 1) as wolf density increased ($R^2 = 0.848$, $F_{[3,8]} = 14.857$, $P = 0.001$; Fig. 1) through time.

Discussion

Our results elucidate six observations that facilitate our understanding of wolf–coyote interactions and coexistence in the YNP ecosystem. First, as predicted wolves are a mortality risk to coyotes; we documented 25 interactions where wolves killed coyotes. Second, 79% of interactions occurred at wolf-killed carcasses as expected, indicating the importance of this carrion source to coyotes. Third, although wolves are the dominant canid (i.e., dominating coyotes in 91% of observed interactions), coyotes do prevail over wolves in certain circumstances. Fourth, in accordance with our expectations, group size possibly mediates outcomes of wolf–coyote interactions. Fifth, in congruence with our prediction, the frequency of interspecific interactions has declined since the reintroduction of wolves, but contrary to our prediction, was negatively correlated with wolf density. These two results viewed simultaneously suggest an adaptive behavioral response by coyotes to the presence of wolves. Finally, no cooperative, amicable, or courtship-related interactions were observed in this study (but see Smith et al. 2001), indicating that hybridization between these canid species is unlikely in YNP. Collectively, these observations provide general descriptions of interspecific interactions between wolves and coyotes, and evidence for the likely alteration of carnivore guilds since the reintroduction of wolves in YNP.

Although anecdotal reports suggest that wolves opportunistically harass and kill smaller carnivores (Ballard et al. 2003), there is little evidence that they actively hunt for them (Paquet 1992; Peterson 1995). Coyotes are reported as the carnivore being most commonly killed by wolves (Palomares and Caro 1999; Ballard et al. 2003). We observed this at low frequency, even though wolf and coyote home ranges frequently overlap (i.e., up to 100%; Arjo and Pletscher 1999; Berger and Gese 2007), and coyotes have been observed to occasionally follow wolves to locate wolf-killed carcasses in YNP and Canada (Paquet 1991), presumably

Table 2. Summary of interaction characteristics categorized by the number of gray wolves (*Canis lupus*) involved.

No. of wolves involved	*n*	Known age class (%)			Initiation (%)			Domination (%)			Wolf kills coyote (rate)
		Breeding adult	Nonbreeding adult	Pup	Wolf	Coyote	Unknown	Wolf	Coyote	Unknown	
1	151	32	36	32	77	19	5	85	11	3	0.02
2	57	37	32	31	84	12	4	91	4	5	0
3	31	38	32	30	94	0	6	100	0	0	0.1
4	18	49	33	18	89	6	6	100	0	0	0.22
≥5	80	29	30	41	95	5	0	98	0	2	0.19

Table 3. Mean number of coyotes (*Canis latrans*) and gray wolves (*Canis lupus*) involved and present during interactions resulting in a coyote death or no coyote death.

	Interactions resulting in						
	Coyote death			No coyote death			
	Mean	SE	*n*	Mean	SE	*n*	*P*
Wolves							
Involved	6.2	0.7	25	2.9	0.2	312	0.0000
Total present	9.2	1.4	25	7.8	0.3	312	0.1108
Coyotes							
Involved	1.4	0.3	25	1.7	0.1	312	0.1245
Total present	2.7	0.6	25	2.2	0.1	312	0.0787

Note: *P* values for the difference (paired *t* tests).

Fig. 1. Gray wolf (*Canis lupus*) density (1995–2007) and wolf – coyote (*Canis latrans*) interactions (1997–2007) on the Northern Range of Yellowstone National Park, Wyoming. Observations and counts recorded during winter study periods. Interactions adjusted for effort (no. of interactions per minute that wolves were in view). In 1995 and 1996, interactions with nonprey were not systematically recorded, therefore were not included.
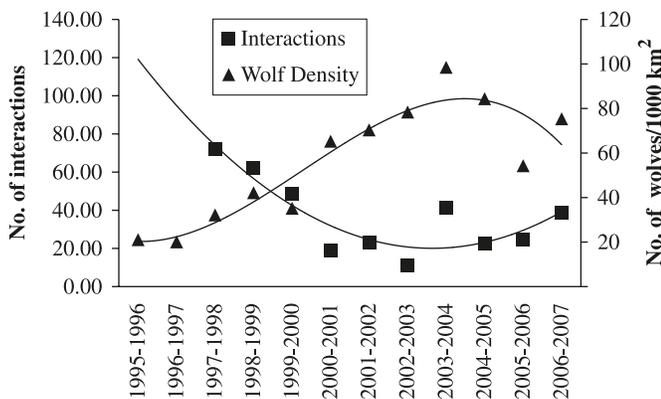
exposing them to greater risk. In YNP, we have not documented wolves feeding on the coyotes they kill, supporting the idea that intraspecific killing is due primarily to competition rather than intraguild predation for food. Crabtree and Sheldon (1999) report a coyote mortality rate of <7.5% from over 200 wolf–coyote interactions in YNP from 1996 through 1998. Our overall coyote mortality rate for wolf–coyote interactions is similar (7%), but may be overrepresented. The rate (4%) provided by winter study data, where effort is recorded and is consistent, may provide a more ac-

curate estimate. The opportunistic observations of interactions during nonwinter study periods may inflate the proportion of fatal wolf–coyote interactions. In addition, our results provide some insight on how coyote mortality rates vary with respect to the number of wolves involved in the interaction. The chances of a coyote getting killed in an interaction is ≤2% when there are <3 wolves involved, and increases to ≥10% when there are ≥3 wolves involved (Table 2). Collectively, these results support the idea of coyote-specific risks being involved when coyotes interact with wolves and that they may vary depending on the number of wolves involved.

The NR of YNP is a unique north temperate grassland, where high grassland productivity supports high densities of ungulates (Smith et al. 2003). Prior to wolf reintroduction, coyotes relied heavily on winter-killed elk carcasses as a food source (Crabtree and Sheldon 1999). However, since wolf reintroduction, available carrion has become more ubiquitous (Wilmers et al. 2003), and coyotes have capitalized on this foraging opportunity. Coyotes have been documented at or within the vicinity of nearly all observed wolf-killed carcasses in YNP (D.W. Smith, personal observation). Likewise, 79% of our observed interactions occurred at wolf-killed carcasses. From these expected observations, it seems clear that the nutritional benefits acquired by coyotes feeding on wolf-killed carcasses may outweigh the risks associated with possible agonistic interactions with wolves. Similarly, the high densities of wolves and coyotes in YNP is presumably attributable to high densities of ungulates that provide abundant carrion sources for scavengers like coyotes.

Coyotes occasionally dominate interactions and we documented 18 interactions where coyotes chased and (or)

attacked/harassed wolves. These instances are initiated mostly by coyotes (94%), occur mostly at neutral sites (72%), and are all dominated by coyotes. Furthermore, of the seven wolf dominated interactions at active coyote dens, coyotes chased or attacked/harassed wolves at some point in four (57%) of those interactions. We did not observe this aggressive behavior from coyotes during other interactions. Thus, in certain circumstances, coyote behaviors that increase risk of injury (i.e., acting aggressively towards wolves) may prevent pup mortality caused by wolves. This agonistic behavior towards potential predators has been commonly noted in canids (e.g., Malcolm and Marten 1982; Peterson et al. 1984).

We observed coyotes occasionally displacing wolves from wolf-killed carcasses for access to carrion. Although we documented displacement of wolves in four interactions, coyotes were much less successful than in the Northern Madison Study Area (NMSA) of Montana (Atwood and Gese 2008). In NMSA, 17 of 36 (47%) agonistic interactions at carcass sites resulted in coyote dominance (Atwood and Gese 2008), whereas we observed 4 of 337 (<1%) in YNP. We suggest three reasons for this discrepancy between study areas. First, our sampling was centered on wolves, therefore we were biased towards wolf-killed carcasses. Atwood and Gese (2008) found coyotes were 5.3 times less likely to supplant wolves from wolf-killed carcasses than from manually placed road-killed carcasses. Secondly, wolf pack sizes in YNP are significantly larger (mean = 10.5; Smith et al. 2004*a*) than the Bear Trap pack (6 individuals; study pack from Atwood and Gese 2008) observed in the NMSA (Atwood and Gese 2008). Consequently, it is less likely that coyote group size could outnumber wolf group size in YNP. Lastly, Atwood and Gese (2008) sampled wolf–coyote interactions from a single wolf pack, so random variation among packs may account for the observed coyote dominance rates. Regardless, this evidence suggests that coyotes have learned methods to gain access to carcasses under wolf possession.

Grouping allows smaller carnivores more access to food and advantages over larger carnivores (Kruuk 1975; Eaton 1979). Coyote social systems are flexible, and in some cases coyotes form larger packs (Camenzind 1978). Crabtree and Sheldon (1999) suggest that coyote group size is important in not being killed by wolves in YNP. Atwood and Gese (2008) found that coyotes outnumbered wolves in 16 of 17 agonistic interactions where coyotes supplanted wolves from carcasses in the MNSA. Our data supports these findings. We documented only one interaction resulting in a coyote death where the involved coyotes outnumbered wolves (Table 1). However, this interaction included a litter of young coyote pups. Of the 18 interactions where coyotes chased and (or) attacked/harassed wolves, wolves did not outnumber coyotes (Table 1), and there were always ≤2 wolves involved in the interaction (Table 2). In addition, 210 (62%) of observed interactions involved a single coyote. Although we did not assess age class of killed coyotes, Berger and Gese (2007) suggest that single transient coyotes are more susceptible to attacks. Thus, wolves may be disproportionally interacting with single coyotes because they are more vulnerable to attack.

Wolf and coyote coexistence is variable across North America. On Isle Royale, Michigan, coyotes were extirpated within a few years after wolf colonization (Mech 1966; Krefting 1969). In Alaska, coyotes that reside within wolf territories have high survival rates (Thurber et al. 1992). In YNP, it appears coyote densities may have fallen since reintroduction (Crabtree and Sheldon 1999; Berger and Gese 2007) and wolves present a mortality risk to coyotes (Berger and Gese 2007; Atwood and Gese 2008), but coyotes have thrived regardless. The coyote's ability to vary its social behavior and adapt and prosper in a diversity of environments (Bekoff and Wells 1986) may explain its continued existence in YNP. Because of wolf-induced mortality risks to coyotes, there may be selection for behaviors that manage the risks associated with wolf presence, particularly those that maximize foraging opportunities from wolf-killed carcasses while minimizing risk of mortality by wolves. Such adaptations include increased vigilance, initiation of aggressive behaviors by socially dominant coyotes, group size adjustments, and differential foraging strategies with respect to carcass consumption stage or season (Atwood and Gese 2008). The inverse relationship of wolf density and interactions (Fig. 1), apart from a possible decrease in coyote density (Berger and Gese 2007), suggests that coyotes quickly adapted to and learned how to avoid interactions with wolves. Our study supports the previously suggested adaptation of increasing group size during interactions with wolves (Crabtree and Sheldon 1999; Atwood and Gese 2008), facilitating continued coexistence.

Hybridization between sympatric coyotes and wolves has been documented (Lehman et al. 1991; Wilson et al. 2000; Kyle et al. 2006). For example, wolves in the Great Lakes and New England regions are of mixed ancestry and include an introgression of coyote genes (Leonard and Wayne 2008), possibly from colonization of coyotes after 1900 (Lehman et al. 1991). It is believed that anthropogenic factors, such as habitat modification and fragmentation, reduction in wolf abundance, and alteration of prey abundance, facilitated colonization and hybridization (Lehman et al. 1991; Leonard and Wayne 2008). In contrast, no hybridization has been documented in western populations of gray wolves and coyotes (Pilgrim et al. 1998). There also has been no evidence of Mexican gray wolves (*Canis lupus baileyi* Nelson and Goldman, 1929) interbreeding with coyotes where they occur in sympatry (Hedrick et al. 1997). Interactions dominated by agonistic or avoidance behaviors documented here and elsewhere (Atwood and Gese 2008), along with greater phenotypic difference in body size (Thurber and Peterson 1991; Way 2007), reduce the likelihood that hybridization will occur, even when wolves are found at low density. In conclusion, understanding individual-level behavioral dynamics of wolf and coyote interactions elucidates mechanisms underlying not only population-level effects, but ecological and evolutionary dynamics of sympatric carnivores in general.

Acknowledgements

ect personnel and winter study volunteers for data collection. We also thank K.M. Berger and P.R. Krausman for reviewing earlier versions of the manuscript.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, **49**: 227–267. doi:10.1163/156853974X00534. PMID:4597405.

Arjo, W.M., and Pletscher, D.H. 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Can. J. Zool. **77**: 1919–1927. doi:10.1139/cjz-77-12-1919.

Atwood, T.C., and Gese, E.M. 2008. Coyotes and recolonizing wolves: social rank mediates risk-conditioned behaviour at ungulate carcasses. Anim. Behav. **75**: 753–762. doi:10.1016/j.anbehav.2007.08.024.

Ballard, W.B., Carbyn, L.N., and Smith, D.W. 2003. Wolf interactions with non-prey. *In* Wolves: ecology, behavior, and conservation. *Edited by* L.D. Mech and L. Boitani. University of Chicago Press, Chicago. pp. 259–271.

Bangs, E.E., and Fritts, S.H. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildl. Soc. Bull. **24**: 402–413.

Bekoff, M., and Wells, M.C. 1986. Social ecology and behavior of coyotes. Adv. Stud. Behav. **16**: 251–338. doi:10.1016/S0065-3454(08)60193-X.

Berg, W.E., and Chesness, R.A. 1978. Ecology of coyotes in northern Minnesota. *In* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York. pp. 158–172.

Berger, K.M., and Gese, E.M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? J. Anim. Ecol. **76**: 1075–1085. doi:10.1111/j.1365-2656.2007.01287.x. PMID:17922704.

Berger, J., Stacey, P.B., Bellis, L., and Johnson, M.P. 2001. A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecol. Appl. **11**: 947–960.

Byrnes, J., Stachowicz, J.J., Hultgren, K.M., Hughes, A.R., Olyarnik, S.V., and Thornbert, C.S. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behavior. Ecol. Lett. **9**: 61–71. doi:10.1111/j.1461-0248.2005.00842.x. PMID:16958869.

Camenzind, F.J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. *In* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York. pp. 267–294.

Canadian Council of Animal Care. 1984. Guide to the care and use of experimental animals. Vol. 2. Canadian Council of Animal Care, Ottawa, Ont.

Carbyn, L.N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Can. Field-Nat. **96**: 176–183.

Caro, T.M., and Stoner, C.J. 2003. The potential for interspecific competition among African carnivores. Biol. Conserv. **110**: 67–75. doi:10.1016/S0006-3207(02)00177-5.

Case, T.J., and Gilpin, M.R. 1974. Interference competition and niche theory. Proc. Natl. Acad. Sci. U.S.A. **71**: 3073–3077. doi:10.1073/pnas.71.8.3073. PMID:4528606.

Coughenour, M.B., and Singer, F.J. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecol. Appl. **6**: 573–593. doi:10.2307/2269393.

Crabtree, R.L., and Sheldon, J.W. 1999. Coyotes and canid coexistence in Yellowstone. *In* Carnivores in ecosystems: the Yellowstone experience. *Edited by* T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva. Yale University Press, London. pp. 127–163.

Creel, S., Spong, G., and Creel, N. 2001. Interspecific competition and the population biology of extinction-prone carnivores. *In* Carnivore conservation. *Edited by* J.L. Gittleman, S.M. Funk, D. Macdonald, and R.K. Wayne. Cambridge University Press, Cambridge. pp. 35–60.

Dekker, D. 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. Can. Field-Nat. **103**: 261–264.

Despain, D.G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Co.

Eaton, R.L. 1979. Interference competition among carnivores: a model for the evolution of social behavior. Carnivore (Seattle), **2**: 9–16.

Estes, J.A. 1996. Predators and ecosystem management. Wildl. Soc. Bull. **24**: 390–396.

Finke, D.L., and Denno, R.F. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecol. Lett. **8**: 1299–1306. doi:10.1111/j.1461-0248.2005.00832.x.

Fritts, S.H., Bangs, E.E., Fontaine, J.A., Johnson, M.R., Phillips, M.K., Koch, E.D., and Gunson, J.R. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. Restor. Ecol. **5**: 7–27. doi:10.1046/j.1526-100X.1997.09702.x.

Fuller, T.K., and Keith, L.B. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. J. Mammal. **62**: 403–405. doi:10.2307/1380725.

Gese, E.M., Ruff, R.L., and Crabtree, R.L. 1996*a*. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool. **74**: 769–783. doi:10.1139/z96-089.

Gese, E.M., Ruff, R.L., and Crabtree, R.L. 1996*b*. Social and nutritional factors influencing the dispersal of resident coyotes. Anim. Behav. **52**: 1025–1043. doi:10.1006/anbe.1996.0250.

Gunther, K.A., Biel, M.J., and Robison, H.L. 2000. Influence of vehicle speed and vegetation cover-type on road-killed wildlife in Yellowstone National Park. *In* Proceedings of the 7th Annual Meeting of The Wildlife Society, Nashville, Tenn., 12–16 Sept. 2000. The Wildlife Society, Bethesda, Md. pp. 42–51.

Haines, A.L. 1977. The Yellowstone story. Colorado Associated University Press, Boulder, Co.

Hebblewhite, M., White, C.A., Nietvelt, C., McKenzie, J.M., Hurd, T.E., Fryxell, J.M., Bayley, S., and Paquet, P.C. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology, **86**: 2135–2144. doi:10.1890/04-1269.

Hedrick, P.W., Miller, P.S., Geffen, E., and Wayne, R.K. 1997. Genetic evaluation of three captive Mexican wolf lineages. Zoo Biol. **16**: 47–69. doi:10.1002/(SICI)1098-2361(1997)16:1<47::AID-ZOO7>3.0.CO;2-B.

Krefting, L.W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist (Leeds), **20**: 24–31.

Kruuk, H. 1975. Functional aspects of social hunting in carnivores. *In* Function and evolution of behavior. *Edited by* G. Baerands, C. Beer, and A. Manning. Oxford University Press, Oxford. pp. 119–141.

Kyle, C.J., Johnson, A.R., Patterson, B.R., Wilson, P.J., Shami, K., Grewal, S.K., and White, B.N. 2006. Genetic nature of eastern wolves: past, present, and future. Conserv. Genet. **7**: 273–287. doi:10.1007/s10592-006-9130-0.

Lehman, N., Eisenhawer, A., Hansen, K., Mech, L.D., Peterson,

R.O., Gogan, P.J.P., and Wayne, R.K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution, **45**: 104–119. doi:10.2307/2409486.

Leonard, J.A., and Wayne, R.K. 2008. Native great lakes wolves were not restored. Biol. Lett. **4**: 95–98. doi:10.1098/rsbl.2007. 0354. PMID:17956840.

Linnell, J.D., and Strand, O. 2000. Interference interactions, coexistence and conservation of mammalian carnivores. Divers. Distrib. **6**: 169–176. doi:10.1046/j.1472-4642.2000.00069.x.

Malcolm, J.R., and Marten, K. 1982. Natural selection and the communal rearing of pups in African dogs (*Lycaon pictus*). Behav. Ecol. Sociobiol. **10**: 1–13. doi:10.1007/BF00296390.

Mech, L.D. 1966. The wolves of Isle Royale. U.S. National Park Service Fauna Ser. No. 7. U.S. Government Printing Office, Washington, D.C.

Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S., and Lamoreux, J.F. 2007. Persistence of large mammal faunas as indicators of global human impacts. J. Mammal. **88**: 1363–1380. doi:10.1644/06-MAMM-A-124R2.1.

Murie, A.M. 1940. Ecology of the coyote in Yellowstone. U.S. National Park Service Fauna Ser. No. 4. U.S. Government Printing Office, Washington, D.C.

Ott, L., and Longnecker, M. 2001. An introduction to statistical methods and data analysis. 5th ed. Duxbury, Pacific Grove, Calif.

Palomares, F., and Caro, T.M. 1999. Interspecific killing among mammalian carnivores. Am. Nat. **153**: 492–508. doi:10.1086/303189.

Paquet, P.C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park. J. Mammal. **72**: 397–401. doi:10.2307/1382113.

Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park. J. Mammal. **73**: 337–343. doi:10.2307/1382067.

Peterson, R.O. 1995. Wolves as interspecific competitors in canid ecology. *In* Ecology and conservation of wolves. *Edited by* L.N. Carbyn, S.H. Fritts, and D.R. Seip. Canadian Circumpolar Institute, Edmonton, Alta. pp. 315–323.

Peterson, R.O., Bailey, T.N., and Woolington, J.D. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. **88**: 1–52.

Pilgrim, K.L., Boyd, D.K., and Forbes, S.H. 1998. Testing for wolf–coyote hybridization in the Rocky Mountains using mitochondrial DNA. J. Wildl. Manage. **62**: 683–689. doi:10.2307/3802344.

Polis, G.A., and Holt, R.D. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. **7**: 151–153. doi:10.1016/0169-5347(92)90208-S.

Pritchard, J.A. 1999. Preserving Yellowstone's natural conditions: science and the perception of nature. University of Nebraska Press, Lincoln.

Rosenzweig, M.L. 1966. Community structure in sympatric carnivore. J. Mammal. **47**: 602–612. doi:10.2307/1377891.

Schmitz, O.J., Hambaeck, P.A., and Beckerman, A.P. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am. Nat. **155**: 141–153. doi:10.1086/303311. PMID:10686157.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. **122**: 240–284. doi:10.1086/284133.

Schullery, P. 1996. The Yellowstone wolves: a guide and sourcebook. High Plains Publishing Comparny, Worland, Wyo.

Schullery, P., and Whittlesey, L. 1992. The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882. *In* Wolves for Yellowstone? Vol. 4. *Edited by* J.D. Varley and W.G. Brewster. National Park Service, Yellowstone National Park, Wyo. pp. 1–4 to 1–174.

Singer, F.J., and Mack, J.A. 1993. Potential ungulate prey for gray wolves. *In* Ecological issues on reintroducing wolves into Yellowstone National Park. *Edited by* R.S. Cook. Monogr. No. NPS/NRYELL/NRSM-93/22. pp. 75–102. Available from U.S. Department of the Interior, National Park Service, Denver, Co.

Smallegange, I.M., van der Meer, J., and Kurvers, R.H.J.M. 2006. Disentangling interference competition from exploitative competition in a crab–bivalve system using a novel experimental approach. Oikos, **113**: 157–167. doi:10.1111/j.0030-1299.2006.14172.x.

Smith, D.W., Murphy, K.M., and Monger, S. 2001. Killing of a bison, *Bison bison*, calf by a wolf, *Canis lupus*, and four coyotes, *Canis latrans*, in Yellowstone National Park. Can. Field-Nat. **115**: 343–345.

Smith, D.W., Peterson, R.O., and Houston, D.B. 2003. Yellowstone after wolves. Bioscience, **53**: 330–340. doi:10.1641/0006-3568(2003)053[0330:YAW]2.0.CO;2.

Smith, D.W., Stahler, D.R., and Guernsey, D.S. 2004*a*. Yellowstone wolf project annual report. Rep. No. YCR-2005-02. Available from Yellowstone Center for Resources, Yellowstone National Park, Wyo..

Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S., and Evans, S.B. 2004*b*. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. J. Wildl. Manage. **68**: 153–166. doi:10.2193/0022-541X(2004)068[0153:WPSAEO]2.0.CO;2.

SPSS Inc. 2005. SPSS® for Windows®. Version 14.0 [computer program]. SPSS Inc., Chicago.

Terborgh, J., Lopez, L., Nunez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., and Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. Science (Washington, D.C.), **294**: 1923–1926. doi:10.1126/science.1064397. PMID:11729317.

Thurber, J.M., and Peterson, R.O. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). J. Mammal. **72**: 750–755. doi:10.2307/1381838.

Thurber, J.M., Peterson, R.O., Woolington, J.D., and Vucetich, J.A. 1992. Coyote coexistence with wolves on Kenai Peninsula, Alaska. Can. J. Zool. **70**: 2494–2498. doi:10.1139/z92-335.

U.S. Fish and Wildlife Service. 1994. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final environmental impact statement. U.S. Fish and Wildlife Service, Helena, Mont.

Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology, **17**: 340–362.

Way, J.G. 2007. A comparison of body mass of *Canis latrans* (coyotes) between eastern and western North America. Northeast. Nat. **14**: 111–124. doi:10.1656/1092-6194(2007)14[111:ACOBMO]2.0.CO;2.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., and Getz, W.M. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. J. Anim. Ecol. **72**: 909–916. doi:10.1046/j.1365-2656.2003.00766.x.

Wilson, P.J., Grewal, S., Lawford, I.D., Heal, J.N.M., Granacki, A.G., Pennock, D., Theberge, J.B., Theberge, M.T., Voigt, D.R., Waddell, W., Chambers, R.E., Paquet, P.C., Goulet, G., Cluff, D., and White, B.N. 2000. DNA profiles of the eastern Canadian wolf and red wolf provide evidence for a common evolutionary history independent of the gray wolf. Can. J. Zool. **78**: 2156–2166. doi:10.1139/cjz-78-12-2156.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall Inc., Upper Saddle River, N.J.