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WOLVES SHARE THEIR ENVIRONMENT with many animals besides those that they prey on, and the nature of the interactions between wolves and these other creatures varies considerably. Some of these sympatric animals are fellow canids such as foxes, coyotes, and jackals. Others are large carnivores such as bears and cougars. In addition, ravens, eagles, wolverines, and a host of other birds and mammals interact with wolves, if only by feeding on the remains of their kills.

Wolves and Guilds

Ecological guilds are groups of species using common resources in a similar way (Root 1967), so wolves are members of a guild that includes other large carnivores, such as bears and cougars. In this chapter, we will also consider birds and mammals that are important scavengers on wolf prey as part of that guild.

Although wolves frequently interact with many other carnivore species and guilds, no studies have been conducted to determine the effects of these interactions on carnivore community structure and population dynamics. Consequently, the only available information concerning wolf-non-prey interactions consists largely of anecdotal observations. In this chapter we review the available literature and data and attempt to synthesize information about interactions between wolves and non-prey animals.

Except for the seminal works of Rosenzweig (1966), Johnson et al. (1996), and Palomares and Caro (1999), few researchers have addressed the subject of carnivore community dynamics, and none has dealt solely with wolves and non-prey species. The inherent genetic, behavioral, and morphological flexibility of wolves has allowed them to adapt to a wide range of habitats and environmental conditions in Europe, Asia, and North America. Therefore, the role of wolves varies considerably among specific ecosystems. To address the community role of wolves within different systems would require in-depth studies of sympatric wildlife populations. For now, we can only review and summarize information about wolf interactions with non-prey and interpret the relevance of these interactions to wolf populations and to the role of wolves within a carnivore and scavenger community or ecosystem.

Interactions among Guild Members

Interactions among members of the carnivore guild are ubiquitous, although opportunities to document such interactions are uncommon due to the elusive nature of most carnivores. The most common type of interaction is probably competition, which is generally most intense between the most similar species (Johnson et al. 1996; Palomares and Caro 1999). The principle of competitive exclusion holds that two competing species may coexist in a stable environment if they have adequate niche differentiation (Krebs 1994). If there is no such differentiation, then one species will exclude the other. The degree of competitive exclusion depends on the degree of niche overlap, the degree of spatial overlap, and the availability of limited resources (i.e., food and space).

Two basic types of competition are recognized: exploitation competition and interference competition.

Exploitation competition is indirect and is based on differential efficiency in accessing and using shared resources. Competition for food is a process in which carnivores interact with one another to access a shared prey base (Murie 1944; Haber 1977; Ballard 1980; Ballard 1982; Boertje et al. 1988) and is a form of exploitation competition. Evidence for such behavior is not always obvious, and it is harder to demonstrate than interference competition. Outcomes of exploitation competition are expressed slowly, through differential survival and reproduction, ultimately leading to extinction or evolutionary divergence (Krebs 1994). Exploitation competition is pervasive and has been predicted in earlier models (Hairston et al. 1960).

Interference competition is direct and is expressed through aggressive behavior. Interspecific killing, for example, is common among mammalian carnivores and may influence population and community structure (Palomares and Caro 1999). Interference competition causes the immediate exclusion of a competing individual or population from a resource (Krebs 1994). Among canids, interference competition is asymmetrical, with only the larger species benefiting from the interaction (Peterson 1995a) by excluding the smaller competitor from the resource. Interspecific competition can also influence spatial patterns in habitat selection and geographic distribution (Connor and Bowers 1987).

Competition, at both individual and population levels, may be influenced in subtle ways. Factors such as different seasonal movements, availability of alternative food resources, topography, snow cover, morphological differences, population characteristics, and reproductive histories may all be important in reducing niche overlap and increasing resource partitioning.

The availability of wolf-killed carcasses in winter tends to concentrate interspecific competition for some species (e.g., coyotes and foxes). Communal feeding at kills by wolves, bears, coyotes, foxes, and common ravens has been observed (Mech 1966b; Peterson 1977; Ballard 1982; Paquet 1992; Peterson 1995a). Such occurrences probably take place when the wolves are satiated and resting and may not truly represent tolerance, but rather the wolves' inability or lack of motivation to chase or catch the scavengers (Peterson 1995a).

As indicated above, degree of niche overlap, food availability, and species behavioral differences influence the intensity of competitive interactions among wolves and other carnivores. Some predators are more robust (i.e., more resilient to random events), can convert available energy into population numbers more quickly, can use food more efficiently, or may have quicker growth rates, than others. Some or all of these characteristics may confer a competitive advantage to one of the interacting species.

We found no case histories in the literature in which competition between wolves and other species resulted in a pronounced and long-lasting spatial partitioning of resources within the same area. There were, however, examples of elimination of some predators (e.g., coyotes) in the presence of wolves because of interference competition (Mech 1966b; Berg and Chesness 1978; Fuller and Keith 1981b; Johnson et al. 1996; Crabtree and Sheldon 1999a).

Most of the descriptions in this chapter discuss events that occur at the individual level and should not be confused with population-level concepts such as the species competition hypotheses used in ecological theory (e.g., ecological niche, principle of competitive exclusion). In addition, observations of individuals should not necessarily be considered important at the population level. Few opportunities have allowed the ecological consequences of competition with wolves to be quantified in terms of ecological theory.

The nature of wolf interactions with non-prey varies according to the size of the animal with which wolves are interacting. Thus we will discuss wolf interactions with different groups of species according to their size.

Interactions with Large Carnivores

The largest non-prey residents of wolf range, such as bears, cougars, and tigers, are competitors, and can even be adversaries, of wolves. Because their sizes, food habits, densities, and other relevant characteristics vary so much, the nature of their interactions with wolves also varies.

Brown Bears

Geographic overlap between wolves and brown (or grizzly) bears was once much more widespread than at present. In Yellowstone National Park (YNP), wolf and brown bear remains were found in the same cave deposits from 960 B.P. (Hadley 1989). Throughout most of their North American and Eurasian ranges, bear populations have experienced human-caused declines in recent years. Nevertheless, brown bears and wolves are still sympatric in significant portions of their former

ranges, and interactions between them have been frequently observed. The most extensive observations come from Alaska and northern Canada.

One of the first biologists to report on interactions between wolves and brown bears was Adolph Murie (1944). He concluded that brown bears easily took ownership of wolf-killed carcasses. Murie did not record any fatal interactions between wolves and bears, although he did describe several harmless skirmishes. Since Murie's pioneering work, many other observations of wolf-bear interactions have been recorded.

We classified wolf-bear interactions into sixteen types of behavior that were modified from classifications originally defined by T. J. Meier and M. D. Jimenez (personal communication). Wolves outnumbered brown bears during 54% of the interactions (table 10.1). Bears outnumbered wolves in only 19% of the interactions, and nearly all of these involved bears accompanied by cubs, yearlings, or 2-year-olds. Most (65%) wolf-bear interactions involved bears without young.

Of the 108 reported interactions between brown bears and wolves (excluding those in YNP), the most common types involved bears and wolves fighting and chasing each other (24%) and bears defending kill sites against wolf packs (see table 10.1). Feeding sites (i.e., kills made by either species) were the most common locations

TABLE 10.1. Summary of wolf-brown bear interactions in North America outside of Yellowstone National Park

	Interaction type[a]																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
No. occurrences	6	7	3	26	11	7	8	1	4	23	2	2	1	2	3	2	108	
% occurrences	6	6	3	24	1	6	7	1	4	21	2	2	1	2	3	2	10	
Type of site																		
Feeding	6	7	3		7			4	23	2	2	1	2	2	2		62	57
Wolf den				13			2										15	14
Other				12	11		6	1							1		31	29
Numbers of each																		
Bears > wolves	1			8	8	1	1		1	1							21	19
Wolves > bears	4	2	1	9	2	6	3	1	3	16	2	2		2	3	2	58	54
Bears = wolves	1	5	1	9	1		3			5							25	23
Unknown			1				1			1			1				4	4
Outcome																		
Bear wins	5	2	1	1	3					22	2					2	38	35
Wolf wins				9	1				4			2			3		19	18
Neither wins	1	4	1	15	7	7	7	1									43	4
Both win		1	1										1				3	3
Unknown				1			1			1				2			5	5
Bears with young																		
Yes	1			10	9		1			3					3		27	25
NA			2	1		7								1			11	10
No	5	7	1	15	2		7	1	4	20	2	2	1	1		2	70	65

Sources: Data sources included Lent 1964; Ballard 1980, 1982; Peterson, Woolington, and Bailey 1984; Hornbeck and Horejsi 1986; Hayes and Mossop 1987; Hayes and Baer 1992; and MacNulty et al. 2001. Also included are previously unpublished data from Denali National Park and Preserve for 1970–1974, 1979–1989, and 1995 (J. W. Burch and T. J. Meier, personal communication), from northwestern Alaska during 1978 (D. James, personal communication), and from the Northwest Territories during 1988 (F. Messier and P. Clarkson, personal communication) and during 1996–1999 (D. Cluff, personal communication). A preliminary analysis of the Denali observations was presented in Servheen and Knight 1993, although locations of observations were not reported.

[a]1, bear feeding, wolf in area, no mortalities; 2, bear and wolf feeding on same kill at same time, no mortalities; 3, bear feeding on wolf kill, wolves not present, no mortalities; 4, bear and wolves fight and chase each other, no mortalities; 5, wolf stalking bear, no mortalities; 6, wolf feeding on bear, believed to be scavenging, but could have been predation; 7, wolf and bear in same area, no mortalities; 8, other, information not specific; 9, wolf displaces bear from kill site, no mortalities; 10, bear defends kill from wolf, no mortalities; 11, bear displaces wolves from kill, no mortalities; 12, wolf defends kill from bear, no mortalities; 13, bear kills animal wounded by wolf, no other mortalities; 14, both bear and wolf sign at kill, cause of death unknown, no mortalities; 15, wolves kill bear; 16, bear kills wolf.

(57%) for all types of interactions. Interactions at a variety of different sites made up the second most common category (29%), followed by those near wolf dens (14%) (see table 10.1). The outcome of wolf-bear interactions varied depending on the type of interaction (see table 10.1). At feeding sites (i.e., kills that could have been made by either species), bears won all (22) of the encounters. Near wolf dens, wolves frequently won. In 3 of the 108 cases, wolves killed bears, and in 2 others, vice versa; most such mortal interactions occurred at feeding sites (see table 10.1).

Wolf-bear encounters can be quite aggressive and may last for several hours, as evidenced by Murie's (1944, 205) account:

> A female with three lusty 2-year-olds approached the den from down wind. They lifted their muzzles as they sniffed the enticing smell of meat, and advanced expectantly. They were not noticed until they were almost at the den, but then the four adult wolves that were at home dashed out at them, attacking from all sides. The darkest yearling seemed to enjoy the fight, for he would dash at the wolves with great vigor, and was sometimes off by himself, waging a lone battle. (On later occasions I noticed that this bear was particularly aggressive when attacked by wolves.) The four bears remained at the den for about an hour, feeding on meat scraps and uncovering meat the wolves had buried. During all of this time, the bears were under attack. When the pillaging was complete the bears moved up the slope.

In YNP, where wolves were recently reintroduced, we suspected that wolf-brown bear interactions might differ from those elsewhere in North America where these relationships have been long established. We found a significant difference in proportions of types of interactions between YNP and other areas in North America (see tables 10.1 and 10.2; $\chi^2 = 114$, $P < .0001$). Some of the differences we found may be rather arbitrary because of our classification system, but some noticeable differences did occur, as we point out below.

The most common interactions between wolves and brown bears in YNP involved wolves and bears simply being in the same area (34%), followed by bears defending kills from wolves (19%; probably wolf kills usurped by bears) and bears usurping wolf kills (19%) (table 10.2). Interactions most often occurred at kill sites (66%).

Most encounters at most sites were won by bears (40%), or the winner could not be determined (40%), even though wolves outnumbered bears during 76% of the interactions. Adult bears without cubs were involved in 88% of the encounters. Although wolves lost most disputed kills to bears, wolves were quite successful at defending their dens, and even wolf pups 6 to 7 months old chased bears away from wolf rendezvous sites (R. McIntyre, unpublished data). Two likely instances of wolves in YNP killing grizzly bear cubs have been recorded. One cub was found near an elk carcass and the other near a bison carcass. Necropsy of the cubs, and the circumstances around the carcasses, indicated death from wolves.

Much less is known about wolf-brown bear interactions in Eurasia, but wolves are known to have attacked young bears. Biologists have concluded that wolves and bears show neither spatial nor trophic influences on each other's distributions (Bromlei 1965; Portenko 1944, cited in Yudin 1992). As in North America, wolves successfully defended their dens against bears (Grachev and Fedosenko 1972).

In all areas, most wolf-brown bear interactions took place near ungulate kills that either predator could have made. Most adult ungulates are probably killed by wolves and then usurped by bears, although bears are also quite capable of killing both young and adult ungulates (Boertje et al. 1988; Ballard et al. 1990). Brown bears commonly usurped kills or defended them from wolves. Younger members of bear families were sometimes killed by wolves at such sites, and wolves were sometimes killed by bears. Wolves sometimes ate bears, but bears usually ate only young wolves.

Such interactions could have profound effects on predator-prey relationships because both wolves and bears can exert considerable pressure on the same prey species. Brown bears are often the greatest source of mortality to moose calves where brown bear densities exceed 16/1,000 km^2 (390 mi^2), even though black bears and wolves may be equally abundant (Ballard 1992). Black bears are the greatest source of moose calf mortality where they are at least ten times more numerous than brown bears or wolves and their densities are greater than 200/1,000 km^2 (Ballard 1992). Where wolves lose kills to bears, their kill rates are probably higher than in systems without bears (Boertje et al. 1988).

The availability of ungulate carcasses to brown bears in systems occupied by wolves undoubtedly results in a higher protein intake for the bears. Reintroduction of

TABLE 10.2. Summary of wolf-brown bear interactions in Yellowstone National Park, Wyoming, during 1996–2001

	Interaction type[a]																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
No. occurrences	0	3	0	7	4	0	20	0	0	11	11	2	0	0	0	0	58	
% occurrences	0	5	0	12	7	0	34	0	0	19	19	3	0	0	0	0	1	
Type of site																		
Feeding		3		2	1		8			11	11						38	66
Wolf den				3	1		6										10	17
Other				2	2		6										10	17
Numbers of each																		
Bears > wolves		1					1			1							3	5
Wolves > bears		2		7	3		13			7	10	2					44	76
Bears = wolves					1		6			3	1						11	19
Unknown																	0	0
Outcome																		
Bear wins				1			1			10	11						23	4
Wolf wins				3	2		1					2					8	14
Neither wins		2		2	2		16			1							23	4
Both win													1				0	0
Unknown		1		1			2							1			4	88
Bears with young																		
Yes		1		2	1		2				1						7	12
NA																	0	0
No		2		5	3		18			11	10	2					51	88

Source: D. W. Smith, unpublished data.

[a]Interaction types as in table 10.1.

wolves into areas such as YNP could provide benefits to rare and threatened bear populations (Servheen and Knight 1993). Such additional protein may aid bear reproduction. Black bear populations with access to relatively high densities of moose calves had higher productivity (Schwartz and Franzmann 1991); the same might be true in wolf-brown bear systems.

Carrion is an important food resource for brown bears upon their emergence from dens in late winter or spring (Servheen and Knight 1993). In YNP before wolf reintroduction, ungulate carrion was not available during mild winters (Houston 1978; Coughenour and Singer 1996). However, during such winters from 1998 to 2001, brown bears were able to usurp wolf kills.

The use of wolf-killed ungulate remains by bears in spring is particularly high in Pelican Valley, where most elk emigrate in winter, but some bison (in numbers dependent on snow depth) remain (Smith et al. 2000). Wolves that kill bison or early-returning elk routinely lose carcasses to brown bears. In one case near Pelican Valley, a brown bear emerged from a den and went directly to a wolf kill. This wolf-bear relationship may become even more important, for some predictions of the results of wolf reintroduction include reduced ungulate numbers (Boyce 1993). This would mean less late winter and early spring carrion, making wolf kills key food sources for brown bears.

In summary, wolf-brown bear interactions appear to involve both interference and exploitative competition. In such systems, ungulate carcasses are probably frequented by both predator species throughout the year. In addition, wolves may feed on bear carcasses, but bears usually eat only the wolf pups.

Black Bears

There are fewer observations of interactions between wolves and black bears ($n = 26$) than between wolves and brown bears, probably because of the different habitats occupied by the two bears. Brown bears live in

open habitats, whereas black bears use dense closed-canopy habitats and are therefore less observable from aircraft. All reported wolf-black bear interactions occurred within the northern portions of black bear range. There are no reported Mexican wolf-black bear interactions, although little was known about Mexican wolves prior to their extermination and subsequent reintroduction in the United States (Ballard and Gipson 2000).

Of the five types of wolf-black bear interactions we classified, wolves killing black bears occurred most often (9 of 26 interactions) (table 10.3). Six of the nine mortalities involved wolves seeking out black bears in their dens, while single bear mortalities occurred at a feeding site, near a wolf den, and at an unclassified site. Only one observation of a black bear killing a wolf was reported, and this occurred near a wolf den.

TABLE 10.3. Summary of wolf-black bear interactions in North America

	Interaction type[a]						
	1	2	3	4	5	Total	%
No. occurrences	9	4	3	9	1	26	
% occurrences	35	15	12	35	4	1	
Type of site							
Feeding	3	2	1	1		7	27
Wolf den	5		1	1	1	8	31
Bear den				6		6	23
Other	1	2	1	1		5	19
Numbers of each							
Bears > wolves	1					1	4
Wolves > bears	5	4	3	9		21	81
Bears = wolves	3					3	15
Unknown					1	1	4
Outcome							
Bear wins	3				1	4	15
Wolf wins	5	2	2	9	0	18	69
Neither win	1	2				3	12
Both win							
Unknown			1			1	4
Bears with young							
Yes	3			6		9	35
NA						0	0
No	6	4	3	3	1	17	65

Sources: Data sources included Young and Goldman 1944; Joslin 1966; Theberge and Pimlott 1969; Rogers and Mech 1981; Horejsi et al. 1984; Paquet and Carbyn 1986; Gehring 1993; Veitch et al. 1993. Also included are unpublished data from Wood Buffalo National Park during 1995 (L. Carbyn, personal communication), Glacier National Park (D. Boyd, personal communication), and Yellowstone National Park during 1997–1999 (D.W. Smith, unpublished data).

[a]1, bears and wolves fight and chase each other, no mortalities; 2, wolf displaces bear from kill site, no mortalities; 3, wolves and bears in same area, no mortalities; 4, wolves kill bear; 5, bear kills wolf.

In 81% of wolf-black bear interactions, wolves outnumbered bears, suggesting that wolves had an advantage in such interactions (see table 10.3). Wolves won 69% of the interactions, while black bears won only 15%. Young black bears were involved in 35% of encounters, which was much higher than the percentage of young bears reportedly involved in wolf-brown bear interactions.

In their review of interspecific killing among all mammalian carnivores, Palomares and Caro (1999) indicated that larger species generally kill both young and adults of smaller species. The outcomes of wolf interactions with brown bears, coyotes, and red and swift foxes fit this pattern, but killings of adult black bears by wolves (Rogers and Mech 1981; Paquet and Carbyn 1986) did not. Wolves apparently sought out black bears in their dens and killed them, only sometimes consuming them. Wolves usually outnumbered black bears in such interactions and won a high percentage of the encounters. Such interactions suggest interference competition between wolves and black bears. Even at kill sites, wolves usurped kills occupied by black bears. These types of interactions contrast sharply with those between wolves and brown bears.

Polar Bears

Wolves and polar bears probably come into contact only rarely (Ramsay and Stirling 1984). During 1980–1983, Ramsay and Stirling (1984) observed six interactions between wolves and polar bears. One interaction involved wolves killing and consuming a bear cub during the bears' spring migration, while another interaction occurred next to a caribou kill adjacent to a polar bear den, although there was no mortality. Both F. Messier (personal communication) and D. Cluff (personal communication) have observed wolves attacking sow polar bears with cubs of the year, but the attacks were unsuccessful. It is doubtful that such interactions are important to either species.

Cougars

Wolves and cougars share geographic ranges along portions of the Rocky Mountains and adjacent mountain

ranges in North America. Both carnivores subsist on ungulates, but they use very different hunting techniques. Cougars are solitary predators and typically do not consume their kills quickly (Murphy 1998).

Since wolf packs are highly mobile, especially in winter, the potential exists for wolves to interact with cougars near kills. The degree of interaction between wolves and cougars probably varies temporally and spatially. In mountainous terrain, winter accumulation of snow often forces common prey species into valleys, which may increase spatial overlap between wolves and cougars (Hornocker and Ruth 1997). During summer, cougars follow prey species to higher elevations, whereas wolves tend to restrict their movements to denning areas in valley bottoms (Hornocker and Ruth 1997; Kunkel 1997).

Although relatively few wolf-cougar interactions have been observed, the animals occasionally do kill each other (Schmidt and Gunson 1985; White and Boyd 1989; Boyd and Neale 1992). Furthermore, usurping of cougar kills by wolves may cause cougars to increase their kill rates (Kunkel 1997; Hornocker and Ruth 1997; Murphy 1998). Based on current data and the paucity of available information, it is doubtful that either wolves or cougars are a significant mortality factor for the other species.

Tigers

Tigers, the largest living felids, overlap the ranges of wolves in Asia. Like other large cats, tigers depend on stealth to kill large prey. They are solitary "stalk and ambush" hunters, exploiting medium-sized to large prey.

In Siberia, prey are scattered, and tiger densities are low (Pikunov 1981; Yudakov and Nikolaev 1987, cited in Yudin 1992). Yudin (1992) suggested that tigers mounted no territorial defense against wolves and that at times, there was a degree of commensalism (Gromov and Matyushkin 1974; Yudin 1992). However, there were other cases in which their interactions appeared to reflect interference competition. Yudin (1992) indicated that there were no known cases of tigers pursuing or killing wolves, but that at least three wolf packs had been displaced by tigers. These observations appear to be an example of spatial partitioning by two carnivore species occupying similar ecological niches on the basis of trophic competition. Whether direct antagonism or predation was involved is unknown because it could well have occurred without being observed.

In fact, this is just what Makovkin (1999) found in the Lazovsky Reserve of the Russian Far East. He indicated that the relationship between wolves and tigers there was dependent on the density of each species, with the tigers outcompeting the wolves. He reported two instances of tigers killing wolves. In one case, the wolf had been wounded by a hunter; in the other, the wolf was killed at an ungulate carcass. In neither case did the tiger consume the wolf (Makovkin 1999). We found no other reports of observations concerning wolf-tiger interactions, but they do warrant further study.

Interactions with Mid-sized Carnivores

Wolf interactions with mid-sized carnivores are dominated by the wolves' superior predatory capacity. Thus the commonest type of interaction with members of this group of non-prey is to chase and attempt to kill them.

Lynx

The ranges of wolves and lynx overlap considerably, but we found only one North American record of a lynx interacting with wolves. In Jasper National Park, a warden watched a lynx feeding at an ungulate carcass for several days; a single wolf nearby did not get a chance to feed at the carcass at any time when the observer was watching (Dekker 1998).

Eurasian lynx are two or three times the size of North American lynx and thus are closer in size to wolves. In Russia, Yudin (1992) described wolf-lynx interactions as highly variable. Apparently there was evidence that wolves and lynx sometimes compete for prey, depending on the prey base. The common prey species for these two carnivores in Europe and parts of Asia is roe deer. In one location, lynx specialized on hares, with roe deer making up only 10–15% of their diet, while wolves specialized on roe deer. Thus, each species exerted a different degree of influence on different prey species. In eastern Poland, competition between wolves and lynx for roe deer was reportedly extensive at times (P. Suminski, personal communication).

Bobcats

We found no report of a wolf-bobcat interaction, although Stenlund (1955) suggested that bobcats benefited directly by scavenging on wolf kills. With the expansion of wolf range into the northwestern and southwestern

United States, opportunities for interaction between wolves and bobcats will probably increase, and may provide opportunities for additional study.

Wolverines

Interactions between wolves and wolverines have been described by a number of researchers (Freuchen 1935; Murie 1963; Burkholder 1962; Boles 1977; Bjärvall and Isakson 1982; Mech et al. 1998; White et al., in press; W. Ballard, personal communication; T. J. Meier, personal communication). Eight of the fourteen documented wolf-wolverine interactions resulted in death for the wolverines. Interestingly, the wolves did not consume the wolverines. Five accounts involved wolves chasing wolverines, but the wolverines reached escape habitats such as trees or caves. The interactions appeared opportunistic in that only three involved wolf kills, one was near a wolverine den, and the other ten occurred away from kills.

Wolf-wolverine interactions can be quite aggressive, as evidenced by an observation made by T. J. Meier during 1987 (Mech et al. 1998, 21):

> In January 1987, pilot Jim Cline and I were radio-tracking the East Fork pack when we spied seven wolves running up a creek bed near the Teklanika River. The wolves overtook and attacked a fleeing wolverine, forming a ring around the animal, lifting it off the ground and shaking it. Making a low pass, we saw that the wolverine was on its back with one wolf continuing the attack. On the next pass, some of the wolves were rolling on the ground, and the others were resting. Several ravens had also arrived. However, we could not find the wolverine.

Meier and Cline searched for 10 minutes.

> The seven wolves eventually arose and moved on up the creek. Finally, after another 20 minutes, we spotted the wolverine running rapidly down the creek the way it and the wolves had come. The creature appeared unhurt, and no blood was visible at the attack site. I visited the scene on the ground the next day. Approaching on the wolves' exit trail, I saw drops of blood in their tracks. At the attack site were a few drops of blood. It appeared that the wolverine had escaped under a shelf of ice until the wolves left. I saw no blood in the wolverine's exit trail, and I believe it escaped unharmed.

Interactions between wolves and wolverines may represent one of the better examples of interference competition. Although most documented interactions between the two species occurred away from wolf kills, we speculate that many of the interactions may have originally begun at kills where wolverines were attempting to scavenge.

Hyenas and Jackals

Although the distributions of wolves overlap with those of hyenas and jackals in Eurasia, there are few published reports of interactions between wolves and these two species. Mendelssohn (1982) reported that wolves and striped hyenas often met at garbage dumps, and that the wolves generally made way for the larger hyenas (weighing 25–40 kg, or 55–88 pounds), but there were occasions when wolf packs displaced hyenas. Wolf interactions with jackals may well be similar to those between wolves and coyotes.

Coyotes

Wolves and coyotes are close relatives (see Wayne and Vilà, chap. 8, and Nowak, chap. 9 in this volume). Although individuals of both species vary greatly in size, coyotes tend to weigh about a third as much as wolves. Many studies indicate that coyote and wolf population densities are inversely related (Berg and Chesness 1978; Paquet 1991b; Thurber et al. 1992; Peterson 1995a), suggesting interference competition. In other areas, the two species may coexist at low densities or remain spatially segregated. Range overlap and killings of coyotes by wolves have been most often documented in winter, when coyotes scavenge on ungulate carcasses (Crabtree and Sheldon 1999a).

The frequency of wolf-coyote encounters might be determined by the availability of food. Coyotes might be largely excluded by wolves where the main food is deer, since wolves are likely to consume all or most of a deer carcass after killing it. Moose and elk, on the other hand, are large enough to satiate a wolf pack and allow scavenging by other species.

Coyote sociality is flexible, and under suitable conditions, coyotes may form packs (Camenzind 1978; Bowen 1978; Gese 1995). Wolves, on the other hand, live in packs of up to forty-two animals (see Mech and Boitani, chap. 1 in this volume), but may become less social

under some conditions and develop more coyote-like lifestyles (e.g., searching for food in pairs or in small packs) (Boitani 1982).

Reports of wolves killing coyotes are common (Seton 1929; Young and Goldman 1944; Munro 1947; Stenlund 1955; Carbyn 1982a; Paquet 1991b; Thurber et al. 1992). Generally, wolf-killed coyotes are not consumed, but rather are left with fatal wounds in the head, neck, rib cage, and back. These wounds often result in massive subcutaneous and internal hemorrhaging, muscle laceration, and trauma. By July 2001, at least twenty-seven coyotes had been killed by wolves in YNP, eighteen (67%) near wolf kills when coyotes approached to scavenge. There are no reported cases of coyotes killing wolves.

Crabtree and Sheldon (1999a) suggested that in YNP, coyote group size is an important factor in avoiding being killed by wolves. Most wolf-coyote interactions there occurred around wolf kills (122 of 145 encounters; 84%), and wolves typically "won" (121 of 145 encounters; table 10.4) these interactions, even when wolf numbers were equal to or less than the number of coyotes (D. W. Smith, unpublished data). Only four instances of coyotes chasing wolves were recorded, and in all four cases, there were at least as many coyotes as wolves. Also, three of these four interactions took place away from kill sites; one to three of them were near a coyote den. Coyotes apparently need special circumstances (e.g., motivation and at least equal numbers) before they will take on wolves. Other, more aggressive interactions have also been observed away from kills. On three occasions wolves attacked coyotes near coyote dens, digging into the dens and killing at least one pup.

TABLE 10.4. Summary of wolf-coyote interactions in Yellowstone National Park, Wyoming, during 1995–2001

	Interaction type[a]					
	1	2	3	4	Total	%
No. occurrences	14	113	17	5	149	
% occurrences	9	76	11	3		1
Type of site						
Kill site	9	99	13	1	122	22
Coyote den	0	1	2	1	4	3
Wolf den	1	2	0	1	4	3
Other	4	11	2	2	19	13
Numbers of each						
Coyotes > wolves	2	13	0	3	18	12
Wolves > coyotes	8	88	17	0	113	76
Coyotes = wolves	3	12	0	2	17	11
Unknown	1	0	0	0	1	1
Outcome						
Wolf wins	3	103	17	0	123	83
Coyote wins	1	1	0	4	6	4
Neither wins	9	9	0	0	18	12
Unknown	1	0	0	1	2	1

Source: D. W. Smith, unpublished data.

[a] 1, No chase, kill, or mortality; 2, wolf chases coyote, no mortality; 3, wolf kills coyote; 4, coyote chases wolf, no mortalities; 5, coyote kills wolf.

It seems significant that only four wolf-coyote interactions took place where a single wolf had denned (not included in table 10.4). This wolf was a subordinate animal bred by the alpha male in the main pack, but she separated from the pack at whelping and denned alone. She produced three surviving pups. Her den was about 16 km (10 mi) from the main pack's den, and wolves from the main pack would occasionally visit her den. Three times in May 2001 coyotes were observed approaching her den. Once, when she was inside the den, a lone coyote carefully approached and raised-leg urinated at the entrance. The coyote left, and the wolf did not exit the den. On two other occasions, one and two coyotes approached her den, and both times she chased them away. In July 2001, when the lone female was not at her den, a coyote encountered one of her pups, chased it, and tackled it twice; however, it did not pursue the pup as it ran off. The pup did not appear injured.

The outcomes of wolf-coyote interactions appear to depend on three related factors: (1) coyotes benefit from scavenging on wolf carcasses; (2) wolves tend to kill coyotes, but do not usually consume them (i.e., killing appears to be opportunistic); and (3) coyotes may space themselves away from wolves (Berg and Chesness 1978; Fuller and Keith 1981b; Carbyn 1982a; Thurber et al. 1992).

Predator control programs in the early 1900s throughout North America greatly reduced or eliminated wolf populations (Young and Goldman 1944), allowing coyotes to expand their range. In addition, agricultural practices provided favorable habitats for coyotes and appeared to increase opportunities for hybridization between wolves and coyotes (Lehman et al. 1991; Roy, Geffen et al. 1994). This process has resulted in a unidirectional introgression of coyote mitochondrial DNA into wolf populations (see Wayne and Vilà, chap. 8, and Nowak, chap. 9 in this volume).

It seems reasonable to conclude that much of the observed wolf-coyote interaction on the individual level is of ecological consequence at the population level for both wolves and coyotes. The implication is that the more closely the interacting species are related, the more significant the long-term ecological consequences.

Can wolves and coyotes coexist in the same area? The answer is not simple. On Isle Royale, colonizing wolves apparently extirpated coyotes just a few years after the wolves arrived on the island (Mech 1966b; Krefting 1969). In other areas (e.g., Riding Mountain National Park), coyotes maintain high densities in the presence of moderate wolf densities (Paquet 1991b; Crabtree and Sheldon 1999a). In Alaska, the survival of coyotes living in wolf range was high (Thurber et al. 1992). Each situation appears to have its own set of dynamics.

Johnson et al. (1996) indicated that the general pattern of canid sympatry throughout most of North America, Eurasia, and Africa involved the occurrence of three sympatric canid species of differing size and forage requirements. In general, the pattern usually consisted of a large (i.e., > 20 kg, or 44-pound) canid, a medium-sized (i.e., 10–20 kg, or 22–44-pound) canid, and a small canid that was more omnivorous than the other species. In North America, this assemblage historically consisted of wolves, coyotes, and red foxes.

In the case of wolves, humans have changed these historical relationships. Wolves and red foxes were sympatric across North America, and coyotes probably occurred mostly along wolf territory boundaries (Fuller and Keith 1981b). In areas where this system was reduced to only two species of canids, as in much of North America when wolves were largely extirpated, several scenarios became possible between coyotes and foxes. These included exclusion, partial exclusion, scattered interspecies territories, or complete overlap (Johnson et al. 1996). Wolf recovery in Glacier and Yellowstone National Parks and on Alaska's Kenai Peninsula resulted in significant changes in coyote numbers, behavior, and distributions (Thurber et al. 1992; Arjo and Pletscher 1999; Crabtree and Sheldon 1999a,b), and probably in similar, but positive, changes in red fox populations.

The current changes within populations of carnivores in YNP as a result of wolf reintroductions present new scenarios that will probably result in long-term changes in the composition of the carnivore guild. There have been several short-term changes in coyote populations in the Lamar Valley of YNP since wolf reintroduction: 25–33% of the coyote population has been killed by wolves each winter; coyote numbers have decreased by 50%; and average coyote pack size has decreased from 6 to 3.8 (Crabtree and Sheldon 1999b). Coyotes in the Lamar Valley have also changed their behavior since wolf reintroduction by denning closer to roads and by reducing the frequency of their vocalizations, behaviors that probably reduce detection by wolves (R. Crabtree, personal communication).

On the other hand, the first record of a wolf and coyotes cooperating, or at least not attacking each other, during the killing of a prey animal was recorded in YNP recently. Four coyotes attacked a bison calf's hindquarters while a wolf bit the animal's neck (Smith et al. 2001). When the calf was dead, the wolf prevented the coyotes from feeding on it.

Wolves no doubt interacted with other canids and carnivores much more extensively in the past (pre-European times), since wolves were present across North America prior to European settlement (Young and Goldman 1944). Coyotes occurred in the more arid regions and open western plains and east to the midwestern states (Nowak 1978). Since the extirpation of wolves from much of their historic North American range, coyotes have greatly expanded their distribution and are now found in nearly every state and province north to Alaska. Possibly wolf elimination from the northern Great Plains influenced coyote densities there, which in turn may have influenced the decline in swift fox numbers (Carbyn 1994).

The question is often raised whether the principle of competitive exclusion is based on similarity of ecological niches. However, Schmidt (1986) pointed out that there is no evidence that aggression between wolves and coyotes is tied to niche overlap. Interference behavior is greatest between species closest in size, regardless of niche overlap, or between species that are most closely related taxonomically.

Interactions with Small Carnivores

Larger species are superior in interference competition, but not in exploitation competition (Persson 1985). This principle holds true for wolf-coyote relationships. Theoretically, smaller animals are likely to be more successful in exploitation competition because the advantage of being small would offset the evolutionary advantages leading to better interference abilities in larger competitors

(Palomares and Caro 1999). Smaller species tend to be more numerous, have smaller home ranges, and exploit resources more efficiently (Palomares and Caro 1999).

Red Foxes

Early explorers and ranchers knew long ago that wolves killed foxes (Young and Goldman 1944). Such behavior has subsequently been documented on Isle Royale in Michigan (Mech 1966b; Peterson 1977; Allen 1979), in Denali National Park and Preserve, Alaska (T. J. Meier, personal communication), and in Wood Buffalo National Park, Alberta (J. Turner, personal communication). The wolves may or may not consume the foxes (Mech 1966b).

Although wolves have killed foxes at a variety of sites and under a variety of conditions, most such mortalities apparently occur near wolf kills where foxes scavenge. T. J. Meier (personal communication) thought that all wolf kills in Denali National Park were ultimately visited by red foxes. Wolf kills undoubtedly provide an important source of food for the foxes. Carbyn et al. (1993) and Peterson (1995a) suggested that competition between red foxes and wolves was less pronounced than competition between coyotes and wolves, and our analyses suggest that wolves kill coyotes more often than they kill red foxes. In Wood Buffalo National Park, Alberta, there was evidence that, in the presence of wolves, fox populations increased (Carbyn et al. 1993). In a second area, Kenai Peninsula, Alaska, Peterson, Woolington, and Bailey (1984) predicted that red fox populations were likely to increase in the presence of wolves.

Arctic Foxes

Little is known about the interaction between wolves and arctic foxes, although there is no reason to believe that such interactions should be any different from those between wolves and red foxes. Wolves do chase arctic foxes whenever they are encountered, and arctic foxes do feed on wolf kills. In one instance, wolves spent considerable time and effort trying to fend off an arctic fox at a fresh muskox kill (Mech and Adams 1999). This was the case even though the wolves were full and were caching and there was still a considerable amount of food left on the carcass.

Interactions with Other Species

It is only natural that a carnivore with such a widespread distribution as the wolf would interact with a wide range of smaller mammalian and avian carnivores. Such encounters have been documented in a variety of anecdotal accounts. For example, Stenlund (1955) and Route and Peterson (1991) reported that river otters were occasionally killed by wolves. D. Boyd (personal communication) found a striped skunk killed by wolves; only the head was consumed. White et al. (in press) reported a single wolf killing an American marten, and L. D. Mech (personal communication) watched a pack of seven arctic wolves chase a weasel. On three occasions, D. Boyd (personal communication) found evidence of wolves killing golden eagles that were attempting to scavenge at ungulate carcasses; none of the eagles was consumed.

In the Great Indian Bustard Sanctuary in Maharashtra State, India, Kumar (1996) observed a pair of wolves with three pups feeding on a road-killed blackbuck near their den. An adult short-toed eagle swooped at the wolves five times. During each swoop, the adult male jumped at the eagle. The fifth time the eagle swooped much lower and was caught and killed by the wolf, but was not eaten. The wolves resumed eating the blackbuck carcass, and later the pack abandoned the carcass, ignoring the dead eagle. The short-toed eagle is not reported to be a scavenger, but feeds on a variety of small mammals up to the size of a hare, so perhaps it was aiming at the wolf pups rather than the carcass (Kumar 1996).

In Poland, Jedrzejewski et al. (1992) reported that wolves regularly inspected raccoon dog and European badger dens and occasionally killed and consumed raccoon dogs. In YNP, five wolves were observed attacking a lone badger (D. W. Smith, unpublished data). Two wolves successively attacked the badger individually, but quickly dropped it. Then all five wolves surrounded the badger, bit it, and violently shook it. The badger appeared to be dead, but two wolves continued to bite it, then carry it. One wolf carried it and dropped it five times before finally leaving it uneaten and joining the other wolves.

The species that probably interacts the most with wolves in North America is the common raven. The two species have a close association, from which the ravens benefit by scavenging wolf kills (Murie 1944; Mech 1966b; Peterson 1977; Carbyn et al. 1993). However, the benefits for the wolves are unclear, and at times wolves

may kill ravens near carcass remains (D. Boyd, personal communication).

One result of wolf-raven interactions can be intense competition for food. Promberger (1992) studied wolf-raven interactions in the Yukon Territory. Sixteen ungulate carcasses were set out for scavengers during late winter, and the biomass of meat taken was measured every 24 hours. Ravens removed as much as 37 kg (81 pounds) of flesh per day. Based on his observations, Promberger estimated that up to 66% of ungulate kills made by single wolves might be consumed by ravens and other scavengers, but only 10% was taken from kills made by wolf packs with ten or more members. At these rates, lone wolves or wolf pairs would have to kill ungulates about twice as often as large packs in order to obtain the same amount of food. Ravens, therefore, when common, could have a considerable effect on wolf kill rates.

Wolf-raven interactions can also have a playful aspect, as indicated by the observations of Mech (1966b, 159) on Isle Royale, Michigan:

> As the pack travelled across a harbor, a few wolves lingered to rest, and four or five accompanying ravens began to pester them. The birds would dive at a wolf's head or tail, and the wolf would duck and then leap at them. Sometimes the ravens chased the wolves, flying just above their heads, and once, a raven waddled to a resting wolf, pecked its tail, and jumped aside as the wolf snapped at it. When the wolf retaliated by stalking the raven, the bird allowed it within a foot before arising. Then it landed a few feet beyond the wolf and repeated the prank.

Recently, Stahler (2000) studied wolf-raven interactions in YNP to determine how much ravens associated with wolves at and away from wolf-killed carcasses. The birds usually stuck close to the wolves while these carnivores were traveling, resting, and hunting. In contrast, ravens did not associate with coyotes or elk or frequent areas that lacked wolves. In Yellowstone, ravens discovered 100% of wolf-killed ungulates in winter.

By associating with wolves, ravens appear to experience a socially facilitated reduction of their fear of large carcasses when first discovered. Stahler (2000) speculated that interactions between wolves and ravens may be important for experience-based modifications of behavior, perhaps built on innate responses, and may ultimately benefit both species throughout their lives. He concluded that these interactions reflected various forms of social symbiosis that hinted at a shared evolutionary history. It is clear that wolf-raven interactions are complex and important and warrant further study.

Wolves interact with a number of other smaller species, but with the exception of foxes and ravens, these interactions are probably opportunistic events that are likely to have an insignificant effect on the species involved.

This evaluation of wolf interactions with non-prey species has revealed a wide range of possibilities. The mechanisms of competition and coexistence between wolves and non-prey species range from interference and exploitative competition and avoidance behavior to tolerance and mutual acceptance. Avoidance behavior becomes important to survival strategies. Tolerance among species of different sizes can be influenced by factors such as food availability, use of different habitats, or temporal segregation in use of the same geographic areas. All of these processes may be of mutual benefit to select species and may help maintain the diversity of ecosystems. Recently, Berger, Stacey et al. (2001) indicated that extirpation of brown bears and wolves from the Greater Yellowstone Ecosystem had resulted in a moose population eruption that altered riparian habitats and caused a reduction in numbers of avian Neotropical migrants. They argued that restoration of bears and wolves provides a management option for restoring biological diversity.

The population characteristics of wolves and their associated non-prey are important in influencing the nature of interspecific competition (Sargeant et al. 1987). Population densities, the presence of adjacent pools of dispersers, reproductive rates, ages of females at first reproduction, and age-specific mortality rates are all important parameters in regulating the outcomes of competition (Sargeant et al. 1987).

During the twenty-first century, wolves will probably become more common in many areas where they once existed. Increasing wolf distributions and reintroductions into historical ranges, along with the development of advanced telemetry systems, better data collection and analytical methods, and more sophisticated research designs may result in a better understanding of the relationships between wolves and non-prey species.

In Yellowstone, cooperative efforts to examine carnivore-carnivore interactions are under way. One study lo-

cated brown bears, cougars, and wolves before and after an elk hunting season on YNP's northern boundary. Preliminary data suggest that each carnivore had a different response to the hunting season: bears were drawn toward hunter activity, cougars moved away, and wolves had no response (D. W. Smith, unpublished data). The next phase of this study includes instrumenting each carnivore with Global Positioning System transmitters so that more locations per day and at night can be obtained.

Despite the competitive nature of the interactions between individuals of competing species, coexistence among carnivores of similar sizes or similar ecological niches does occur. The ranges of wolves, bears, coyotes, and foxes overlap in many areas where the species coexist in the same ecological systems. Wolves can exclude coyotes, and coyotes can exclude red foxes, at a number of scales ranging from individual encounters and territories to entire regions, yet they all coexist over many regions of North America (Crabtree and Sheldon 1999a). Wolves have been eliminated in many other parts of the world (see Fritts et al., chap. 12, and Boitani, chap. 13 in this volume), so the absence of this apex predator must also have created changes in the structures of ecosystems there. Conversely, in some parts of Europe, wolf populations are now extending their ranges into formerly occupied regions, probably causing more such changes in the opposite direction.