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DIETARY OVERLAP BETWEEN WOLVES AND COYOTES IN NORTHWESTERN MONTANA

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We studied effects of recolonizing wolves (*Canis lupus*) in the North Fork of the Flathead area of northwestern Montana on the diets of coyotes (*C. latrans*) from 1994 to 1997. Wolf and coyote diets differed in frequency of occurrence of prey species during 3 of the 4 summers and winters ($P < 0.001$) during the study. Coyote diets contained more murid prey items, and wolf diets contained more deer (*Odocoileus virginianus* and *O. hemionus*) in the summer and elk (*Cervus elaphus*) in the winter. Coyotes and wolves ate prey of different size during both the summer ($P < 0.001$) and winter ($P < 0.001$) months in 1994–1996: wolves took a greater proportion ($P < 0.001$) of large (>45 kg) prey species and coyotes, small (<2 kg) prey ($P < 0.001$). Wolves selected a larger proportion of adults ($P < 0.001$), whereas coyotes selected a larger proportion of juveniles ($P < 0.001$) during summer. We believe that differential use of food resources facilitates coexistence of wolves and coyotes in the North Fork of the Flathead area.

Key words: coexistence, coyote, food habits, Montana, partitioning, recolonization, wolf

Distribution and abundance of carnivores in western United States has changed drastically over the last century. Although originally sympatric, gray wolves (*Canis lupus*) and coyotes (*C. latrans*) did not coexist in Montana for 50 years (Ream and Mattson 1982), as a result of campaigns to exterminate predators in the early part of the 20th century. Wolves began to recolonize the Flathead area in northwestern Montana just north of Glacier National Park in 1982 (Ream et al. 1991). Competition may limit coyotes as wolf populations increase.

Coexistence is usually facilitated by morphological differences, such as size, between sympatric species (Krebs 1978). Differences in body size are often related to the prey consumed (Gittleman 1985; Rosenzweig 1966). Larger predators can kill and consume both large and small prey and thereby increase diversity in their diets. Wolves usually feed on large ungulate species but can kill most vertebrate species within their home range (Gittleman 1985; Mech 1970; Paquet 1992). Coyotes usually rely on small mammals (Gese et al. 1996; Theberge and Weledes 1989; Thurber et al. 1992). Coyotes are opportunistic and generalist predators (Bowyer et al. 1983; Gier 1975; Ozoga and Harger 1966) that can feed on ungulates (Andelt et al. 1987; Gese and Grothe 1995; Teer et al. 1991). Much of the ungulate remains in the coyote scats, however, may be the result of feeding on carrion (Berg and Chesness 1978; Ozoga and Harger 1966; Weaver 1979).

Coexistence of similar canids partially depends on environmental productivity and diversity (Johnson et al. 1996). The competitive exclusion theory implies that coexistence of closely related species depends on resource partitioning and the degree to which shared resources are limited (Gause

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1934). Because interference competition in canids is asymmetrical (Peterson 1995), limited resources may cause a shift in niche use or, in extreme cases, competitive exclusion of the subordinate species. Major and Sherburne (1987) documented low dietary overlap during most of the year between red foxes (*Vulpes vulpes*) and coyotes as a result of the specialization on prey that reflected predator body size. During summer and autumn, however, when fruits were available, dietary overlap increased. High dietary overlap between red foxes and coyotes was also observed in Yukon Territory where snowshoe hares (*Lepus americanus*) were the primary food resource for both canids (Theberge and Weldes 1989). Although dietary overlap occurred, lower densities of foxes were able to persist with coyotes through spatial partitioning and elasticity of prey choice (Major and Sherburne 1987; Theberge and Weldes 1989).

Voigt and Berg (1987) noted that where prey is limited in the winter sympatric species might have overlapping diets, especially when ungulates are the primary food resource. Litvaitis (1992) argued that additional quantitative information through experimentation on the extent of prey overlap is needed and that wolf recolonization of the northern Rocky Mountains may provide such an opportunity. We examined whether resource partitioning allowed for coexistence of coyotes with wolves in an area recently recolonized by wolves. We made 3 predictions that coyotes would avoid competing with wolves for food resources by using smaller prey items, that coyotes would have a greater diversity in their diet, and that coyotes within established wolf territories would scavenge on large mammals more than coyotes outside wolf territories.

Materials and Methods

Study area.—We conducted this study in northwestern Montana along the North Fork of the Flathead River drainage, from the Canadian border south to the Apgar Mountains. The North Fork River divides Glacier National Park on the east side from the Flathead National Forest, Coal Creek State Forest and from private lands on the west side of the 3,000 km^2 study area. The valley bottom (4–10 km wide) ranges in elevation from 1,374 m in the north to 1,024 m in the south. The Whitefish Range borders the North Fork Valley on the west and the Continental Divide borders the valley on the east.

Habitat was diverse, ranging from dry, forested sites to meadows and relatively moist valley bottoms. Although subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*) were present in the valley, the dominant cover was lodgepole pine (*P. contorta*). Riparian areas were dominated by spruce (*Picea*) and black cottonwood (*Populus trichocarpa*—On and Shaw 1979). Snow usually remained on the ground from mid-November through mid-April, and total snowfall varied widely: 306 cm in 1994, 51 cm in 1995, 76 cm in 1996, and 356 cm in 1997. For analysis of scavenging, winters with deep snow (1993–1994 and 1996–1997) were combined, as were winters with less snow (1994–1995 and 1995–1996). Maximum average daily temperatures at Polebridge, Montana, ranged from −2.2°C in January to 27.3°C in July, and average minimum daily temperatures ranged from −13.2°C in January to 5.0°C in July for 1994–1997.

The North Fork area in northwestern Montana is 1 of the last ecosystems in the contiguous United States still containing a full complement of predators that were present during pre-Columbian America. Not only does the North Fork area contain the highest density of grizzly bears (*Ursus arctos*) in the lower 48 states (McLellan 1989) but it is also the 1st area in the western United States where gray wolves successfully recolonized. Numbers of wolves in the area increased steadily over the years, reaching a plateau of approximately 32 wolves in 1993 (Pletscher et al. 1997). Black bears (*U. americanus*), cougars (*Puma concolor*), coyotes, and wolverines (*Gulo gulo*) comprise the rest of the large mammalian predators in the area. The coyote population declined in the study area between 1991 and 1997 (Arjo and Pletscher 1999). Midsized mammalian predators in the area included bobcats (*Lynx rufus*), lynx (*L. canadensis*), and fisher (*Martes pennanti*). Ungulate prey species in the Flathead Valley included elk (*Cer-

vus elaphus), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Smaller mammalian prey species included beaver (*Castor canadensis*), snowshoe hare, mountain cottontail (*Sylvilagus nuttalli*), Columbian ground squirrel (*Spermophilus columbianus*), red squirrel (*Tamiasciurus hudsonicus*), and various species of murids.

Food habits from carcasses.—Food habits for coyotes and wolves were determined by locating kills in the winter and by analyzing scats. We backtracked wolves and coyotes during the winters of 1994–1995, 1995–1996, and 1996–1997 (November through March) to locate kills. In addition, backtracking on wolf and cougar tracks was done by personnel working on concurrent studies of cougars (T. Ruth, pers. comm., for period 1994–1997) and ungulates and wolves (K. Kunkel, pers. comm., for period 1992–1995). Thus, additional ungulate carcass and scavenging information were obtained. Each carcass was examined for cause of death, age, and species of prey killed. When tracks were not distinguishable for determining species of predator, we examined carcasses for evidence indicating methods of killing, which could be used to identify the predator involved (Kunkel 1997). We determined frequency of coyote scavenging on wolf and cougar kills from tracks present at carcasses and used a z-test (Zar 1996) to test whether frequency of coyote scavenging was similar across prey species (elk, deer, and moose).

Food habits from scats.—We determined food habits from 617 wolf scats and 279 coyote scats collected from 1994 to 1997. Scats were collected along roads, trails, den sites, and at rendezvous sites. We relied on presence of tracks or other predator sign in the area to distinguish wolf from coyote scats. Scats >30 mm in diameter were considered wolf scats and scats <25 mm in diameter were considered coyote scats (Weaver and Fritts 1979). Scats 25–30 mm in diameter were discarded unless other evidence was available, such as tracks, to determine the source. The majority of the wolf scats collected in summer, when confusion between wolf pups and coyotes could potentially occur, were collected at wolf dens and rendezvous sites. Each scat was categorized by season. Spring and summer (summer, from 15 April, the beginning of denning, through 30 September) were combined because of inaccessibility of dens and rendezvous sites before September when canids abandoned them. Sample size (n) in the autumn was small, so we combined scats from autumn and winter (winter, 1 October through 14 April).

Scats were autoclaved, washed in a sieve to separate hair and bone fragments from the rest of the material, and then allowed to air dry. We identified prey species macroscopically from tooth, claw, and hoof fragments found in the scats. Impressions of dorsal guard hairs containing the basal portion were used for microscopic identification (Moore et al. 1974).

We estimated frequency of occurrence (100 times the number of occurrences of a food item divided by the total number of occurrences of all food items) for both canid species for each year and season. Coyote scats collected inside the core home range of wolf packs were classified as inside wolf territories; others were considered outside wolf territories. Core areas were defined as the 62% adaptive-kernel contour determined by two-thirds of the maximum-probability contour (home range) used (Shivik et al. 1996). We used a chi-square contingency-table analysis to test for differences in coyote scats inside and outside wolf territories by season, to compare coyote diets by year, and to compare coyote versus wolf scats by year. Data were lumped for all years if individual chi-square tests showed no significant difference. We used a z-test to test where differences occurred when chi-square showed significant differences. We adjusted chi-square analyses using Yates' correction factor when $d.f. = 1$ (Zar 1996).

Resource partitioning by canids was estimated using Horn's (1966) similarity index (R_o) to calculate coyote and wolf dietary overlap (summer and winter, by year). In addition, to determine if coyotes had an increase in diversity of diet to compensate for overlap with wolf territories, Shannon's diversity index was calculated for each canid species and a t-test was used to compare diversity of diets by species (Zar 1996).

Age and size of prey.—We used chi-square analysis to compare ages (juvenile and adult) of ungulates selected during the summer by wolves and coyotes. In addition, a chi-square contingency-table analysis was used to determine whether wolves and coyotes partitioned prey by size in winter and summer for each year. Prey items were classified into 3 categories: prey < 2 kg; 45 kg > prey > 2 kg; prey > 45 kg (following Bowen 1981; Gese et al. 1988; Meleshko 1986). Average mass for each ungulate species was estimated from the literature (Dusek et al. 1989; Franzman et al. 1978; Weaver 1994). These data were combined with ratios of females to males among all elk and deer during summer from the North Fork area (Bureau 1992; Langley 1993; Rachael 1992) to compute an average adult size. Weights from Burt and Grossenheider (1976) were used for small mammals. Prey in the smallest category included mustelids, rodents, and leporids. Average weights for newborn fawns (Robbins and Moen 1975), elk calves (Cook et al. 1996), and moose calves (Franzman et al. 1978; Peterson 1955) placed them in the middle category. Beavers and coyotes were also grouped in the middle category. Adult ungulates, and moose and elk calves after July, comprised the heaviest category. We used a z-test to test for differences in the use of size categories of prey between coyotes and wolves when the chi-square value showed significant differences. All tests were considered significant at the probability level of $P \leq 0.05$.

RESULTS

Food Habits from Carcasses

We found 152 wolf kills (winter 1993–1994, collected by concurrent research projects, $n = 62$; 1994–1995, $n = 41$; 1995–1996, $n = 19$; 1996–1997, $n = 26$). Deer comprised the largest proportion (74%) of wolf kills during winters (Kunkel et al. 1999). Coyotes scavenged wolf kills more frequently than they scavenged cougar kills. Wolf-killed elk ($z = -3.68$, $P < 0.001$) and wolf-killed moose ($z = -3.75$, $P < 0.001$) were scavenged more frequently than wolf-killed deer. Coyotes also scavenged more in the milder winters of 1994–1995 and 1995–1996 ($z = -5.2$, $P < 0.001$) than in the deep-snow winters of 1993–1994 and 1996–1997.

We did not find many coyote kills, and those found were usually large prey (no remains were usually left when a coyote fed on small mammals). Ten deer (including 1 fawn) comprised the coyote-killed ungulates for 1994–1997. Two red squirrels, a snowshoe hare, 2 grouse (*Bonasa umbellus* and *Dendragapus obscurus*), and a mallard (*Anas platyrhynchos*) made up the remaining kills discovered.

Food Diets from Scat Analysis

Coyote diets inside and outside wolf territories.—Summer food habits on the basis of scats of coyotes inside wolf territories ($n = 46$) were similar to those of coyotes outside ($n = 102$) wolf territories ($\chi^2 = 5.49$, $d.f. = 6$, $P = 0.51$); however, in winter, food habits of coyotes inside ($n = 36$) and outside ($n = 95$) wolf territories were different ($\chi^2 = 9.28$, $d.f. = 4$, $P = 0.044$). Coyotes inside wolf territories used a greater proportion of deer and lagomorphs than did coyotes outside wolf territories. Coyote scats collected outside wolf territories contained a greater proportion of elk.

Comparison of coyote and wolf diets.—We divided food items into 8 categories to compare coyote and wolf diets for 1994–1997: deer, elk, moose, murids, squirrels, other rodents, lagomorphs, and miscellaneous food items. The most common species in the other-rodent category was beaver; however, northern pocket gophers (*Thomomys talpoides*) and yellow pine chipmunks (*Tamias amoenus*) also appeared in wolf diets. Miscellaneous food items included insects, vegetation, coyotes, avian remains, 2 instances of domestic cow (in the coyote diet), a marten (*Martes americana*, in the coyote diet), and a long-tailed weasel (*Mustela frenata*, in the wolf diet; Tables 1 and 2). We found coyote hair in coyote scats but believe it was incidentally ingested from grooming; therefore, we did not include it in analyses.

Coyote diets from 1994 to 1997 differed from year to year during winter ($\chi^2 = 71.5$, $d.f. = 3$, $P < 0.001$) and summer ($\chi^2 = 38.5$, $d.f. = 6$, $P < 0.001$). Coyotes depended on rodents (murids and squirrels) in the winters of 1994 and 1995 and more heavily on ungulates during the winters of 1996 and 1997. Murids (mostly *Microtus*) comprised the largest portion of the coyote summer diet in 1994 and 1995; ungulate use increased in 1996 and 1997. Wolf diets

TABLE 1.—Frequency of occurrence of food items in coyote scats from 1994 to 1997 in northwestern Montana.

	1994				1995				1996				1997			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
Taxa	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mammalia																
Lagomorph																
Leporidae																
Lepus americanus	1	2.9	0		4	7.6	0		18	11.8	11	21.6	1	5.0	5	8.1
Sylvilagus nuttalli	0		0		1	1.9	1	1.9	3	2.0	1	2.0	0		0	
Ochotonidae																
Ochotona princeps	0		0		0		0		0		0		0		0	
Rodentia																
Sciuridae																
Tamiasciurus hudsonicus	2	5.7	0		0		0		1	0.7	0		0		1	1.6
Tamias amoenus	0		0		0		0		0		0		0		0	
Spermophilus columbianus	6	17.1	0		6	11.3	1	1.9	14	9.1	0		2	10.0	0	
Castoridae																
Castor canadensis	3	8.6	1	3.5	1	1.9	2	3.8	1	0.7	0		0		0	
Geomyidae																
Thomomys talpoides	0		0		0		0		0		0		0		0	
Muridae																
Peromyscus maniculatus	0		0		4	7.6	1	1.9	5	3.3	0		0		0	
Microtus	14	40.0	25	86.2	12	22.6	16	30.2	25	16.2	7	13.7	1	5.0	1	1.6
Unknown rodent	1	2.9	0		1	1.9	0		1	0.7	3	5.9	0		0	
Insectivora																
Soricidae																
Sorex	0		0		0		1	1.9	0		0		0		0	
Artiodactyla																
Cervidae																
Odocoileus	5	14.3	2	6.9	10	18.9	17	32.1	45	29.2	21	41.2	4	20.0	12	19.4
Cervus elaphus	0		0		3	5.7	4	7.6	12	7.8	3	5.9	11	55.0	33	53.2
Alces alces	1	2.9	1	3.5	2	3.8	1	1.9	14	9.1	3	5.9	1	5.0	8	12.9

TABLE 1.—Continued.

Taxa	1994				1995				1996				1997			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Carnivora																
Mustelidae																
Martes americana	0		0		0		1	1.9	0		0		0		0	
Mustela frenata	0		0		0		0		0		0		0		0	
Canidae																
Canis latrans	0		0		2	3.8	0		1	0.7	0		0		2	3.2
Aves	1	2.9	0		0		1	1.9	4	2.6	1	2.0	0		0	
Insecta	0		0		4	7.6	5	9.4	3	2.0	0		0		0	
Planta	0		0		3	5.7	2	3.8	5	3.3	1	2.0	0		0	
Other	1	4.3	0		0		0		1	1.3	1	3.0	0		0	
Total number of scats	23		26		33		29		77		33		15		43	

also differed yearly in winter ($\chi^2 = 28.9$, *d.f.* = 9, $P < 0.001$) and summer ($\chi^2 = 94.5$, *d.f.* = 15, $P < 0.001$).

Food habits were compared by year because of variability of both coyote and wolf diets. Summer food habits differed between wolves and coyotes in 1994 ($\chi^2 = 39.4$, *d.f.* = 3, $P < 0.001$), 1995 ($\chi^2 = 49.5$, *d.f.* = 4, $P < 0.001$), and 1996 ($\chi^2 = 59.4$, *d.f.* = 4, $P < 0.001$) but not in 1997 ($\chi^2 = 0.08$, *d.f.* = 1, $P = 0.71$). Deer were more important in wolf diets than in coyote diets, whereas murids in 1994–1996, squirrels in 1994 and 1996, and lagomorphs in 1995 and 1996 were more important in coyote diets.

Diversity indices were different for all 4 years; wolves had greater diversity in their diet in 1994 ($t = -2.10$, *d.f.* = 58, $P = 0.04$) and 1997 ($t = -5.64$, *d.f.* = 14, $P < 0.001$), and coyotes in 1995 ($t = 3.03$, *d.f.* = 168, $P = 0.003$) and 1996 ($t = 3.28$, *d.f.* = 359, $P = 0.01$). Horn's overlap was relatively high every year (1994, $R_o = 0.72$; 1995, $R_o = 0.85$; 1996, $R_o = 0.87$; 1997, $R_o = 0.78$).

Winter food habits were different between coyotes and wolves in winters with less snow: 1994–1995 ($\chi^2 = 18.5$, *d.f.* = 3, $P < 0.001$) and 1995–1996 ($\chi^2 = 30.2$, *d.f.* = 3, $P < 0.001$). We found murids more frequently in coyote than in wolf scats during these years. Deer in 1995 and elk in 1996 were found more frequently in wolf diets than in coyote diets. Sample size was too small in 1994 to analyze without violating the assumptions of the chi-square test. Food habits of wolves and coyotes were similar in 1997 ($\chi^2 = 0.58$, *d.f.* = 3, $P = 0.90$). Horn's overlap index was generally high but varied greatly (1994, $R_o = 0.25$; 1995, $R_o = 0.85$; 1996, $R_o = 0.71$; 1997, $R_o = 0.92$), and Shannon's diversity index was different between coyotes and wolves only in 1996 ($t = 3.83$, *d.f.* = 96, $P < 0.001$) when diversity of coyote scats was greater.

Age and size of prey.—Because of the small sample size we pooled data across

TABLE 2.—Frequency of occurrence of food items in wolf scats from 1994 to 1997 in northwestern Montana.

	1994				1995				1996				1997			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
Taxa	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mammalia																
Lagomorph																
Leporidae																
Lepus americanus	0		0		5	1.6	1	2.1	2	1.0	1	1.9	5	4.7	0	
Sylvilagus nuttalli	1	1.0	0		5	1.6	0		2	1.0	0		0		0	
Ochotonidae																
Ochotona princeps	0		0		1	0.3	0		1	0.5	0		0		0	
Rodentia																
Sciuridae																
Tamiasciurus hudsonicus	0		0		0		0		2	1.0	0		0		0	
Tamias amoenas	0		0		0		0		1	0.5	0		0		0	
Spermophilus columbianus	0		0		21	6.5	0		4	2.1	0		0		0	
Castoridae																
Castor canadensis	17	17.4	1	1.4	13	4.0	1	2.1	8	4.1	1	1.9	3	2.8	1	3.2
Geomyidae																
Thomomys talpoides	0		0		3	0.9	0		0		0		0		0	
Muridae																
Peromyscus maniculatus	0		0		6	1.9	0		0		0		0		0	
Microtus	1	1.0	0		6	1.9	5	10.6	2	1.0	0		2	1.9	0	
Insectivora																
Soricidae																
Sorex	0		0		0		0		0		0		0		0	
Unknown rodent	0		0		2	0.6	0		0		0		0		0	
Artiodactyla																
Cervidae																
Odocoileus	60	61.2	40	54.8	142	44.0	27	57.5	117	60.0	27	50.0	50	47.2	6	19.4
Cervus elaphus	3	3.1	20	27.4	37	11.5	7	14.9	26	22.2	22	40.1	18	17.0	16	51.6
Alces alces	10	10.2	8	11.0	70	21.7	5	10.6	22	11.3	2	3.7	12	11.3	6	19.4

TABLE 2.—Continued.

Taxa	1994				1995				1996				1997			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Carnivora																
Mustelidae																
Martes americana	0		0		0		0		0		0		0		0	
Mustela frenata	0		0		0		0		0		0		1	0.9	0	
Canidae																
Canis latrans	1	1.0	2	2.7	2	0.6	0		3	1.5	1	1.9	1	0.9	1	3.2
Aves	3	3.1	0		4	1.2	0		3	1.5	0		0		0	
Insecta	1	1.0	0		1	0.3	0		1	0.5	0		1	0.9	0	
Planta	1	1.0	0		1	0.3	0		1	0.5	0		13	12.3	1	3.2
Other	0		0		0		0	6.4	0		0		0		0	
Total number of scats	76		43		200		33		141		33		70		21	

years to compare age of ungulate prey in summer. Coyotes and wolves used ungulate prey of different age in the summer (χ^2 = 76.4, *d.f.* = 1, $P < 0.001$). Coyotes took a greater proportion of juveniles than did wolves (z = 8.8, $P < 0.001$), and wolves took a greater proportion of adults (z = −8.7, $P < 0.001$).

Partitioning of foods by size also occurred in both winter and summer diets. Vegetation only in the form of seeds and berries was considered in this analysis because other vegetation, such as grasses, was probably ingested incidentally. We found that coyotes and wolves partitioned summer prey by size in 1994 (χ^2 = 61.96, *d.f.* = 2, $P < 0.001$), 1995 (χ^2 = 58.98, *d.f.* = 2, $P < 0.001$), and 1996 (χ^2 = 97.1, *d.f.* = 2, $P < 0.001$) but not in 1997 (χ^2 = 1.03, *d.f.* = 3, P = 0.61). Wolves generally relied more on large species (ungulates) and coyotes on species <2 kg in body weight (murids and squirrels). We pooled categories of medium-sized and small prey for winter diet analysis because of the small sample size of medium-sized prey. Size partitioning in winter was different between the species in 1994 (χ^2 = 74.3, *d.f.* = 1, $P < 0.001$), 1995 (χ^2 = 15.46, *d.f.* = 1, $P < 0.001$), and 1996 (χ^2 = 27.1, *d.f* = 1, $P < 0.001$) but not in 1997 (χ^2 = 0.92, *d.f.* = 1, P = 0.38). Wolves relied on larger prey than did coyotes. Coyotes in 1997 used larger prey than they did in the previous years.

DISCUSSION

Scavenging can be a reliable method for obtaining food at a reasonably low level of energetic expenditure. Nonetheless, it can incur considerable costs such as aggressive encounters with larger predators (Major and Sherburne 1987; Paquet 1992). In some areas coyotes obtain the majority of their diet from scavenging (Bekoff and Wells 1980; Gese and Grothe 1995; Paquet 1992). Coyotes scavenged both wolf and cougar kills and chose the larger ungulates, moose and elk, over deer. Boyd et al. (1994) found that wolf-killed ungulates were more completely consumed in mild winters than in severe winters, and deer were consumed more than elk. To compensate for the risk of scavenging, coyotes increase their energy benefits by scavenging the larger ungulates (elk and moose) that usually have more carrion left on them than wolf-killed deer. In addition, coyotes before wolf colonization were found to be mostly single animals or pairs (Boyd 1982). After wolf recolonization the majority of the coyotes were found as pairs or small packs (Arjo 1998). We believe that the addition of a large food source, wolf-killed elk and moose, has allowed for the increased size in coyote social groups (Arjo and Pletscher 1999). In addition, scavenging was greater in mild winters of 1994–1995 and 1995–1996. Coyotes are more successful in killing ungulates in deep snow than in shallow snow (Gese and Grothe 1995; Huegel and Rongstad 1985; Ozoga and Harger 1966) and may have scavenged more on wolf kills during mild winters to compensate for their decreased ability to capture large prey. Coyotes in our study area before wolf recolonization relied on lagomorphs and small mammals (Boyd 1982). Ungulates, especially elk and moose, were relatively unavailable to coyotes then, and winter mortality was not a significant factor for the ungulate population. Coyotes consumed ungulates much more frequently during our study than before wolf recolonization (Arjo and Pletscher 1999). This added food source is advantageous to the coyotes in that it allows for another source of prey previously unattainable. Before wolf colonization coyotes relied mainly upon lagomorphs (Boyd 1982). Although wolves relied only slightly on this prey species, the availability of lagomorphs to coyotes has decreased from historical times. The loss of lagomorphs as an important coyote prey item may now be offset by the addition of ungulates to the coyote diet.

Leopold and Krausman (1986) and Litvaitis and Harrison (1989) documented changes in predator diets caused by the presence of a competing predator. Coyote diets in our study area were different within wolf territories from those outside wolf territories, during winter. Deer were more prevalent in coyote diets within wolf territories, probably as a function of scavenging by coyotes even though we found that elk and moose, when available, were preferred by coyotes. During the severe winter of 1996–1997, ungulates became a major food source for coyotes both inside and outside wolf territories. The deep snows impeded ungulate movement and increased winter mortalities in both areas. Coyote home ranges were usually located along the edge of wolf territories; however, during winter, overlap of home ranges increased (Arjo and Pletscher 1999). The difference in coyote diets inside wolf territories compared with that outside wolf territories exemplifies the opportunistic foraging behavior that allows coyotes to coexist with wolves.

In Alaska, Thurber et al. (1992) reported little overlap in canid diets because wolves use moose, whereas coyotes primarily consume small mammals. In Riding Mountain National Park, Manitoba, Meleshko (1986) showed extensive overlap between coyote and wolf diets in their use of ungulates and that small mammals comprise an insignificant portion of the coyote diet. High overlap in diets of wild dogs (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*) in Africa, however, leads to exploitative competition and a negative correlation between wild dog and hyena densities (Creel and Creel 1996). Although dietary overlap between coyotes and wolves was high, diversity of diets was usually different. Diversity indices are not only affected by number of prey categories but also by distribution of prey within each category (Zar 1996). A more diverse diet is represented by several categories of prey with relatively equal distribution throughout the categories. High dietary overlap may contribute partially to the decline observed in coyote densities in the North Fork area because there is an increased demand on all prey species with the increase in wolf population. In addition, the ungulate populations declined during the study period (Kunkel et al. 1999). Dietary diversity, however, may help to negate this overlap.

Exploitative competition may occur when diets are similar. Species can coexist with high overlap if diversity is greater in 1 species' diet (White et al. 1995), if prey are partitioned by size (Rosenzweig 1966) or differential use (Mills 1984), or if prey are abundant. In northern latitudes, prey diversity is limited in winter, which can lead to an increase in dietary overlap between sympatric predators (Litvaitis 1992; Voigt and Berg 1987). Coyote and wolf diets, for both summer and winter, were different every year, except in 1997 when use of ungulates increased in the coyote diets. Ungulates were the primary source of food in coyote winter diets in 1996 (deer) and 1997 (deer and elk). Occurrence of elk in coyote scats was likely influenced by the severe winter of 1997 and by increased mortality of ungulates. During summer, coyotes could rely on both small mammals and fawns, but in winter, diets of the 2 canid species became more similar because coyotes relied more on ungulates in the absence of available microtines during winters of deep snow. Bowen (1981), Hamilton (1974), and Meinzer et al. (1975) found that diversity in coyote diets usually increases in summer when smaller mammal species are more available. The addition of murids and squirrels to the coyote diet during summer may have allowed overlap in ungulate prey species and continued coexistence of the 2 species in our study.

Competitors may use different prey sizes to decrease competition for food resources. Meleshko (1986), in Riding Mountain National Park, and Manitoba and Stebler (1951), in Minnesota, found that wolves and coyotes partition prey by size. Coyotes and wolves in the North Fork area used different size of prey, with coyotes focusing on prey items <2 kg in body weight and wolves on large ungulates. White et al. (1995) hypothesized that endangered San Joaquin kit fox (*V. macrotis mutica*) are able to coexist with coyotes even with high dietary overlap because they partition food by size. Similar results were seen in central Kentucky where coyotes kill and consume larger prey than do red foxes (Crossett 1990).

Another method of partitioning prey resources is by differential use of prey age classes. Craig (1986) and Koehler and Hornocker (1991) found that competition among carnivores was offset by use of similar prey items in different proportions. Although deer were usually the dominant food item in wolf diets and most dominant food item (or at least the 2nd most dominant) in the coyote diets in this study, proportional use between the 2 canids was almost always significantly different (deer were used in lower proportion in the coyote diet than in the wolf diet). In addition, coyotes obtained most of their ungulate diet from scavenging (differential use), a mechanism similar to that which allows extensive spatial overlap and coexistence between coyotes and wolves in Riding Mountain National Park (Meleshko 1986; Paquet 1992). Differential use by partitioning prey by age can also decrease competition. Mills (1984) showed that lions (*Panthera leo*) and spotted hyenas in the southern Kalahari partition similar prey, the gemsbok (*Oryx gazella*), by age; lions kill adults and hyenas kill juveniles. Differential use of similar ungulate prey was seen in coyotes and wolves in the North Fork area. Coyotes used proportionally more juvenile elk and deer, whereas wolves used more adults.

Paquet (1992) suggests that coexistence between coyotes and wolves would be low in areas where deer are preferred because of the potential loss of scavenging by coyotes when entire carcasses are consumed. Deer were the preferred prey of wolves in the North Fork area, and deer populations declined throughout our study (Kunkel et al. 1999). We documented interference competition in the study area inside wolf core areas (at least 3 coyotes were killed by wolves—Arjo 1998), and in some years wolves left the coyotes little to scavenge. We believe that coyotes and wolves in the North Fork area are able to coexist and feed on similar prey items using several partitioning methods. Coyotes and wolves used different age and size classes of prey, coyotes exploited alternative prey (small mammals) during summer, and coyotes scavenged during winter. In addition, when coyotes and wolves converge on ungulate species during winter, coyotes can temporally or spatially avoid larger predators (Arjo and Pletscher 1999). Coyote populations did, however, coexist at lower levels than they did before wolf recolonization, probably because of increased competition and demand on available prey resources and interference competition. Before wolf reintroduction, coyotes in Yellowstone National Park (Gese et al. 1996) relied heavily on winter-killed elk as a food resource. Gese et al. (1996) also found differential use between coyote pack members on small mammal prey. We believe that coyotes and wolves in Yellowstone National Park will also be able to coexist as a result of the ability of coyotes to exploit other prey resources such as small mammals.

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