WINTER PREY SELECTION BY WOLVES AND COUGARS IN AND NEAR GLACIER NATIONAL PARK, MONTANA

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Abstract: Expansion by wolf (*Canis lupus*) populations in the western United States creates new opportunities and challenges for researching and managing large mammal predator–prey systems. Therefore, we compared patterns of prey selection between wolves and cougars (*Puma concolor*) to ascertain the effects of multiple predators on prey and on each other. Because of differences in hunting techniques, we predicted that wolves would kill more vulnerable classes of prey than cougars. Our results did not support this prediction. White-tailed deer (*Odocoileus virginianus*) composed the greatest proportion of wolf (0.83) and cougar kills (0.87), but elk (*Cervus elaphus*) and moose (*Alces alces*) composed a larger proportion of wolf (0.14, 0.03, respectively) than cougar (0.06, 0.02, respectively) kills. Wolves and cougars selected older and younger deer and elk than did hunters. Cougars killed relatively more bull elk (0.74) than did wolves (0.48). Male deer killed by cougars had shorter diastema lengths than did male deer killed by wolves ($P = 0.02$). Pack hunting by wolves and dense stalking cover may have partially explained the failure to support predictions of the coursing versus stalking dichotomy. Wolves and cougars may be exhibiting exploitation and interference competition that is affecting each others' behavior and dynamics, and that of their prey.

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Wolves and cougars top the terrestrial food chain in North America. These 2 predators greatly influence the communities they inhabit, especially their cervid prey base (Bergerud 1988, Berger and Wehausen 1991, Hatter and Janz 1994, McNay and Voller 1995, Boertje et al 1996, Wehausen 1996), and together might be considered keystone predators (Mills et al. 1993, McLaren and Peterson 1994). These predators were widespread and their ranges overlapped extensively before European settlement of the continent. With recent wolf recolonization and restoration, wolves and cougars have again become sympatric within and near Glacier and Yellowstone National parks and in central Idaho. The natural experiment created by wolf restoration in those areas presents interesting ecological questions and management opportunities.

Selection of prey is of primary interest in the ecology and management of predators and their prey. Canids and felids generally use different hunting techniques: coursing (canids) versus stalking (felids). This dichotomy in hunting techniques suggests that prey selection should differ between the 2 groups. Success for canids should be more dependent on prey condition, a factor that should be less important for felids. Evidence from Africa for the coursing versus stalking dichotomy among large carnivores is sparse and contradictory (Kruuk 1972, Schaller 1972, Reich 1981, Fitzgibbon and Fanshawe 1989). In these studies, habitat, prey species, and prey behavior had as much influence as hunting technique on selection of prey by predators.

Sympatric wolves and cougars provide another test of the stalking versus coursing dichotomy. Wolves rely on speed over relatively long distances to overtake prey (Mech 1970), whereas cougars rely on surprise and short pursuits to capture prey (Hornocker 1970). Therefore, we hypothesized that a greater proportion of prey killed by wolves would be less fit than prey killed by cougars. However, because cougars hunt singly, whereas wolves hunt in packs, we also hypothesized that wolves should be more successful at killing larger species of prey than are cougars (Nudds 1978, Sunquist and Sunquist 1989, but see Schmidt and Mech 1997).

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Using reviews of the literature, Weaver (1994) concluded that wolves specialize on elk and moose, and Anderson (1983) concluded cougars specialize on deer.

Examination of prey selection by sympatric wolves and cougars and of the factors influencing selection could aid in predicting the effects of these predators on prey populations and on each other as the geographic range of overlap between wolves and cougars expands. Limiting effects of predation on prey populations may be greater where these predators occur in sympatry than where either occurs alone, because prey may have greater difficulty escaping predation when they live with predators that use different hunting strategies (Kotler et al. 1992). Partitioning of prey because of interference and exploitation competition between wolves and cougars could produce additive effects by these 2 predators on prey populations.

We examined predation by wolves and cougars within and near Glacier National Park from 1992 to 1996 to determine species, sex, age, and condition of prey selected. We predicted that, relative to cougars, wolves would (1) kill a greater proportion of less robust classes of prey, including fawns and calves (Mech 1970), males (Mech 1970, Clutton-Brock et al. 1982), and senescent animals; (2) kill a greater proportion of prey in poorer nutritional condition (Mech 1996); and (3) kill more larger prey species (elk, moose).

STUDY AREA

The core of the approximately 1,000-km^2 study area in the basin of the North Fork of the Flathead River was the northwestern quarter of Glacier National Park in Montana. The Whitefish and MacDonald Divide formed the western border of the study area, and the Livingstone Range and Continental Divide formed the eastern border. Between the divides, the approximately 100-km valley of the Flathead River varied from 4 to 10 km in width and from 1,024 to 1,375 m in elevation. Land east of the the Flathead River (south of Canada) was managed by Glacier National Park. West of the river, land ownership was a mosaic of Flathead National Forest, Coal Creek State Forest, and private property. The British Columbia portion of the study area was composed primarily of Crown (federal government) lands. Density of humans was <0.005 people/km^2 in British Columbia and <0.1 people/km^2 in Montana.

The climate is transitional between the northern Pacific coastal and the continental types. Mean temperatures ranged from −9°C in January to 16°C in July (Singer 1979). Snow normally covered the area from mid-November to mid-April. The annual maximum snow depth at the Polebridge Ranger Station averaged 65 cm (Singer 1979). Dense lodgepole pine (*Pinus contorta*) forests dominated most of the valley, but sub-alpine fir (*Abies lasiocarpa*), spruce (*Picea* spp.), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*) communities existed throughout the valley. Abundant meadows and riparian areas were dispersed throughout the study area. Detailed descriptions of vegetation communities in this area were provided by Jenkins (1985) and Krahmer (1989).

Approximately 10 wolves/1,000 km^2 and 70 cougars/1,000 km^2 occur in the North Fork basin (winter density occurring in a portion of the study area; K. E. Kunkel and T. K. Ruth, unpublished data). Grizzly bear (*Ursus arctos*) density was estimated to be 64/1,000 km^2 for the Canadian portion of the study area (McLellan 1989), and black bear (*Ursus americanus*) density was estimated to be approximately 200/1,000 km^2 (B. N. McLellan, British Columbia Ministry of Forests, personal communication).

METHODS

During 1992–96, wolves were captured, sedated with 4 mg/kg of tiletamine HCl and zolazepam HCl administered from a jabstick, and radiotagged (Mech 1974, Ream et al. 1991). We located wolves from the ground or the air >4 times/week during winter (Nov–Apr) in the U.S. portion of the study area to identify their travel routes. We located kills made by wolves by following these travel routes on skis or snowshoes 1–2 days after wolves had left the area.

Cougars were captured with hounds released on cougar tracks (Murphy 1998). Treed cougars were immobilized with 8.4 mg/kg of ketamine hydrochloride and 0.47 mg/kg xylazine hydrochloride fired from a dart rifle and then radiotagged (Hornocker and Wiles 1972). Cougars whose signals were audible from roads or trails were located daily from the ground, and all cougars were located weekly from the air. We located kills made by cougars by snowtracking radiotagged cougars, by following cougar tracks during capture efforts, and occasionally by following travel routes of wolves. When capturing and handling wolves and cougars, we followed protocols approved by the University of Montana Animal Care and Use Committees.

Deer carcasses for which there were not enough remains to determine species were classed as white-tailed deer when they were discovered in white-tailed deer winter ranges. Sex of elk and deer carcasses was determined by presence of antlers or pedicels, length of hind foot (Fuller et al. 1989), or pelvic characteristics (Edwards et al. 1982). An incisor, if present, was extracted to estimate age (Matson's Lab, Milltown, Montana, USA); otherwise, age was based upon tooth eruption and wear (Severinghaus 1949), skull size, or length of hind foot.

We considered predation to be the cause of death when blood, subcutaneous hemorrhaging at wound sites, or sign of a struggle was found at the site. We used tracks, scats, hair, and disposition of the carcass as evidence to determine the species of predator responsible (O'Gara 1978) and, when present, other species visiting or scavenging the carcass. We developed a key based on these characteristics and the work of others (Hatter 1984, Whitten et al. 1985; T. K. Ruth, unpublished data) to categorize wolf and cougar kills as either certain, probable, or possible. Only kills categorized as certain or probable were used in analyses.

We collected femur marrow, when present, from each carcass. These samples were double-wrapped in plastic and kept frozen until analysis. We used oven-dry mass (60°C for 48 hr) of the marrow expressed as a percentage of its wet mass to estimate percent fat (Neiland 1970). We measured diastema length on each carcass as an additional estimate of condition (Reimers 1972, Frisina and Douglass 1989).

Species, sex, age, and month of kills were cross-tabulated by predator responsible. We used Pearson chi-square analysis to test the null hypotheses of independence among categories. When >20% of cells had expected values <5, we combined adjacent categories (e.g., deer ≥6 yr old). Adjusted standardized residuals [(observed − expected/expected$^{0.5}$)/standard error] were computed to identify significant cells (Habermann 1973). Probability values used for determining significance were adjusted by dividing by the number of cell pairs in the cross-tabulation (Bonferroni adjustment: e.g., overall $P < 0.10$ and cell pairs = 5, 0.10/5 = 0.02; Miller 1981:219).

We used systematic transects to estimate relative proportions of available prey. Sixteen systematic transects (approx 7 km each) followed hiking trails and roads dispersed throughout the study area. Each of these routes was usually followed once in early winter and once in late winter. Data from all winters (1993–96) were pooled. Relative densities of prey were estimated at 1-km intervals by skiing 2 100-m transects in opposite directions perpendicular to the trail or road (n = 696 transects). We recorded distance to the first white-tailed deer, elk, and moose track on each transect. The number of deer, elk, and moose tracks located on both transects (0, 1, or 2; only the first track for each species was recorded) was divided by the distance to that track (e.g., 1/190 if 1 deer track was found at 90 m in 1 direction and no deer track was found along the opposite 100-m transect) to obtain the number of deer, elk, and moose tracks per meter. This value was divided by the number of days since the most recent snowfall of >5 cm to adjust for snowfall effects. When snowfall had not occurred for ≥7 days, we divided the value by 7 because we assumed that track deposition had plateaued after 7 days and tracks started to deteriorate.

We calculated Manly's (1974) α for each prey species by using the constant prey population method to estimate dietary preference of wolves and cougars:

$$\alpha = \frac{r_i}{n_i} \times \frac{1}{\sum (r_j/n_j)},$$

where r_i, r_j = proportion of prey i or j in the diet (i and j = 1, 2,. . ., m); n_i, n_j = proportion of prey type i or j in the environment; and m = number of prey species possible. Alpha values were normalized such that their sum = 1.0. Thus, if predation is nonselective, α = 1/m; if a prey item is preferred, α > 1/m. Standard errors of the alpha values were estimated, and hypothesis tests of differences between alpha values were conducted following Equations 5 and 8 of Manly (1974).

We operated the hunter check station in the study area each year to estimate the age and sex composition of hunter-killed deer and elk; we also measured the diastema length of each animal. Hunters could harvest bucks and bull elk throughout the 5-week hunting season (late Oct through Nov). Does could be harvested the first 8–15 days of the season (depending on the

Table 1. Species of prey selected by wolves and cougars in and near Glacier National Park, Montana, 1992–96.

	Wolf				Cougar[a]				Systematic transects	
			Manly's α				Manly's α			
Species	%	n	$\bar{x}$	SE	%	n	$\bar{x}$	SE	%	Tracks/km
White-tailed deer	83	138	0.49	0.01	87	118	0.69	0.01	74	14.8
Elk	14	23	0.38	0.02	06	8	0.22	0.04	16	3.2
Moose	03	5	0.14	0.04	02	2	0.09	0.08	10	1.9

[a] Wolves versus cougars (χ^2_2 = 6.10, P = 0.048).

year), and cow elk could be harvested only the first 8 days. Beginning in 1994, cow elk could be taken only by permit, and 20 permits were issued. Because regulations biased harvest toward males, we only conducted 1-way tests between predator and hunter selection for sex (e.g., reported significance if predator selection was more male-biased than hunter selection).

Ages and femur marrow fat of prey killed were not normally distributed, so medians were compared via Kruskal-Wallis and Mann-Whitney U-tests. We determined differences between diastema lengths of prey killed by wolves, cougars, and hunters via analysis of covariance (ANCOVA), using age of prey (months alive) as the covariate.

We used multiresponse permutation procedures (MRPP; Mielke et al. 1976) to compare distributions of locations (Universal Transverse Mercator coordinates) of wolf kill sites to locations of cougar kill sites and to compare locations of cougar kill sites we found by snowtracking wolves to locations of cougar kill sites we found by snowtracking cougars. Multiresponse permutation procedures compare the average intragroup distances of locations with the average distances that would have resulted from all other possible combinations of the data under the null hypothesis of no difference in distributions. The MRPP does not require normality or equal variances between groups (Zimmerman et al. 1985). The P-values (calculated via program BLOSSOM [Slauson et al. 1994. User manual for BLOSSOM statistical software, unpublished. National Biological Survey, Ft. Collins, Colorado, USA.]) indicate the probability that the spatial distribution of wolf kills and cougar kills were the same.

RESULTS

We followed 30 radiotagged wolves in 3–4 packs from May 1992 to April 1996. Aerial counts made in May of each year indicated packs consisted of 5, 11, 3, and 4 wolves in 1992; 10, 7, 5, and 6 in 1993; 11, 3, and 7 in 1994; 10, 4, and 10 in 1995; and 12, 5, and 6 in 1996. Most carcasses we located were remains of kills made by wolves in the South Camas (first numbers above) and North Camas packs (second numbers above) south of the Canadian border. We followed 40 radiotagged cougars from December 1992 to April 1996.

From 1992 to 1996, we found 138 wolf-killed white-tailed deer, 23 wolf-killed elk, 118 cougar-killed white-tailed deer, and 8 cougar-killed elk. The number of elk kills located from 1992 to 1996 was too small to analyze, so we augmented the sample with an additional 68 wolf kills and 8 cougar kills found from 1984 to 1991 in the same area. These kills were located by backtracking wolves, and only those classed as "certain" wolf or cougar kills were included. We found 23 wolf-killed and 2 cougar-killed moose, and 1 wolf-killed and 7 cougar-killed mule deer (*Odocoileus hemionus*). Mule deer samples were too few for analysis. Hunters brought 270 white-tailed deer and 204 elk through the check station during the 1991–95 hunting seasons.

The spatial distributions of cougar kills resulting from kills located by backtracking wolves versus backtracking cougars were similar (Δ = −0.96, P = 0.12). We found no difference in the spatial distribution of wolf kills versus cougar kills (P = 0.35). From 1986 to 1996, cougars visited or scavenged 11 (2.9%) of 381 wolf kills, while wolves visited or scavenged 33 (20.1%) of 164 cougar kills (χ^2_1 = 36.89, P < 0.001).

Timing of wolf versus cougar kills did not differ by months over the course of winter for either white-tailed deer (χ^2_3 = 1.53, P = 0.67) or elk (χ^2_2 = 2.72, P = 0.26). The relative proportion of deer, elk, and moose in wolf and cougar kills differed (P = 0.048; Table 1). Elk made up a marginally greater proportion of wolf kills (0.14) than cougar kills (0.06; Z = 2.20, P = 0.08).

Table 2. Ages of white-tailed deer killed by wolves, cougars, and hunters in and near Glacier National Park, Montana, 1992–96.

Age	Wolf-killed			Cougar-killed			Hunter-killed		
	M	F	Total	M	F	Total	M	F	Total
<1	8	8	16	16	16	32	8	13	21
1–2	8	7	15	9	9	18	98	35	133
3–5	11	6	17	12	8	20	75	30	105
6–7	4	4	8	5	3	8	3	5	8
8–9	2	2	4	4	5	9	2	0	2
10+	1	9	10	0	3	3	2	0	2
Total	34	36	70	46	44	90	188	83	271

Deer tracks were 4.6 times more frequent than elk tracks and 7.8 times more frequent than moose tracks encountered on systematic transects (Table 1). When compared with availability of prey along systematic transects, wolves preferred (Manly's α of 0.33 = no preference) deer over elk (P = 0.014) and moose (P < 0.001) and preferred elk over moose (P < 0.001). Cougars also preferred deer over elk (P < 0.001) and moose (P < 0.001, respectively) and preferred elk over moose (P = 0.042).

Age

Deer.—The age distribution of male deer killed by wolves and cougars did not differ (χ^2_3 = 1.25, P = 0.74; Table 2). The age distribution of wolf and hunter kills differed (χ^2_3 = 23.22, P < 0.001). Wolves killed more fawns (P < 0.001) and ≥6.5-year-old deer (P < 0.001) and fewer 1.5–2.5-year-old deer (P = 0.002) than did hunters. The age distribution of cougar and hunter kills also was different (χ^2_3 = 63.13, P < 0.001). Cougars killed more fawns (P < 0.001) and ≥6.5-year-old deer (P < 0.001), and fewer 1.5–2.5-year-old deer (P < 0.001) than did hunters.

There was no difference between the age distribution of female deer killed by wolves or cougars (χ^2_4 = 3.31, P = 0.51), but hunters differed from wolves (χ^2_4 = 34.23, P < 0.001) and cougars (χ^2_4 = 23.79, P < 0.001). More ≥6.5-year-old female deer were killed by wolves (P < 0.001) and cougars (P = 0.002) than by hunters. Fewer 1.5–2.5-year-old deer were killed by wolves (P = 0.02) and cougars (P = 0.02) than by hunters. Cougars also killed more fawns (P = 0.009) than did hunters.

The median age of female deer killed by wolves (5.0) was older (U = 463.0, P = 0.077, n = 70) than that of males killed by wolves (3.5). There was no difference in the median age of male and female deer killed by cougars (2.0 vs 2.5; U = 992.0, P = 0.869, n = 90).

Elk.—The age distribution of elk (sexes combined, 1984–96) killed by wolves was similar to that killed by cougars (χ^2_3 = 5.41, P = 0.14; Table 3). The age distribution of elk killed by wolves (χ^2_3 = 34.51, P < 0.001) and cougars (χ^2_3 = 27.35, P < 0.001) was different from hunters. Versus hunters, wolves (P < 0.001) and cougars (P = 0.01) killed more calves. More >9-year-old elk were killed by wolves (P = 0.02) and cougars (P < 0.001) than by hunters. Fewer 1–3-year-old elk were killed by wolves (P = 0.01) and cougars (P = 0.004) than by hunters. Wolves killed less 4–9-year-old elk than hunters (P = 0.003).

Table 3. Age and sex of elk killed by wolves, cougars, and hunters in and near Glacier National Park, Montana, 1986–96.

Age and sex	Wolf-killed n	Cougar-killed n	Hunter-killed n
<1	35	7	17
1–3	35	5	83
4–9	15	5	52
>9	12	7	7
M	35	17	113
F	38	5	91

Sex

The sex ratio of deer killed by wolves (0.46 M; Table 2) was similar to that killed by cougars (0.49 M; χ^2_1 = 0.10, P = 0.75). Cougars killed a greater proportion of male elk (0.74, n = 17) than did wolves (0.48, n = 35; χ^2_1 = 4.75, P = 0.03) and hunters (0.55, n = 113; χ^2_1 = 2.90, P = 0.09). There was no difference between the sex ratio of wolf and hunter kills (χ^2_1 = 1.2, P = 0.274).

Nutritional Condition

Male deer killed by cougars had shorter diastema lengths ($\bar{x}$ = 67.7, SE = 2.5, n = 13) than did male deer killed by wolves ($\bar{x}$ = 71.4, SE = 2.3, n = 21; $F_{1,32}$ = 12.0, P = 0.002) and hunters ($\bar{x}$ = 73.5, SE = 0.59, n = 157; $F_{1,168}$ = 7.46, P = 0.007). The length of wolf-killed and hunter-killed diastemas was similar ($F_{1,175}$ = 1.80, P = 0.182). We found no difference in diastema lengths of female deer killed by wolves ($\bar{x}$ = 69.9 mm, SE = 1.7, n = 16), cougars ($\bar{x}$ = 70.3 mm, SE = 1.8, n = 22), or hunters ($\bar{x}$ = 66.6 mm, SE = 0.9, n = 81; $F_{1,35}$ = 1.8, P = 0.19).

There was no difference in the femur marrow fat of male or female deer killed by wolves or cougars (males: 0.63, SD = 0.32, n = 28 vs. 0.73, SD = 0.25, n = 25 [P = 0.88]; females: 0.82, SD = 0.25, n = 30 vs. 0.85, SD = 0.25, n = 27 [P = 0.41]). Sample sizes were too small for femur marrow fat and diastema comparisons in elk.

DISCUSSION

Prey Selection

We found little support for the differences in prey selection that were hypothesized to result from the different hunting techniques used by the 2 predators. Wolves and cougars selected deer over elk and killed deer of similar age, sex, and condition. We might have underreported the number of fawns killed by wolves, because wolves occasionally completely consume fawns.

We found, similar to many studies (wolves: Mech 1996; cougars: Robinette et al. 1959, Hornocker 1970, Spalding and Lesowski 1971, Shaw 1977, Ackerman et al. 1984, Murphy 1998), that wolves and cougars primarily killed the most vulnerable individuals in the population (e.g., old, young, or with marrow fat indicative of animals of reduced vigor or vitality; Mech et al. 1995). Alternately, O'Gara and Harris (1988) found cougars killed primarily male deer in prime condition (based on age and femur fat consistency). They speculated that male mule deer in their prime used habitats that exposed them to greater cougar predation risks. We agree with Mech (1996) that traits predisposing prey to wolves (and other carnivores) are subtle and not easily measured. That both wolves and cougars are selecting the most vulnerable prey suggests that the similarity in prey selection between the 2 may largely result from the ambushing predator being more dependent on substandard prey than hypothesized. Cougars must still subdue and kill large and potentially dangerous prey once they are ambushed. As a result, cougars are more likely to be successful killing less fit individuals.

Wild dogs (*Lycaon pictus*) in the Serengeti killed a greater proportion of gazelles (*Gazella thomsoni*) in poor condition than did cheetahs (*Acinonyx jubatus*), as is predicted by the hunting dichotomy (Fitzgibbon and Fanshawe 1989). However, Fitzgibbon and Fanshawe (1989) speculated that this occurrence may have resulted from factors unrelated to condition. They also postulated that wild dogs did not kill more young and old gazelles than did cheetahs, because cheetahs were able to distinguish vulnerable animals without chasing them.

Hunting in packs by wolves and the relatively dense stalking cover in our study area may partially explain why our evidence was contrary to predictions of the hunting dichotomy. Hunting in packs may allow wolves to take less vulnerable prey than cougars, which have to bring down large and dangerous prey. The benefits of hunting in packs, at least up to a point (pairs or small groups), have been reported by several researchers who found a positive relation between wolf pack size and kill rate (Messier and Crete 1985, Ballard et al. 1987, Sumanik 1987, Thurber and Peterson 1993, Dale et al. 1995). These researchers speculated that larger packs had reduced handling and search times and higher energy demand compared to smaller packs. However, as indicated by Mech (1966, 1988), it is the adult pair that press most attacks, and thus the primary benefit is probably accrued by the advantage of 2 versus 1 wolf attacking. Additionally, the rugged topography and dense vegetation of northwestern Montana probably results in relatively short chases by wolves, thereby reducing selection for less fit individuals (Reich 1981, Okarma 1984, Huggard 1993; K. E. Kunkel, unpublished data). Under these circumstances, wolves probably stalk their prey to close distances and then use a quick rush over a relatively short distance (Mech 1970)—a tactic similar to cougars.

In multiprey systems where elk are as or more abundant than deer, greater differential prey selection between wolves and cougars may occur. Given equal encounter rates, wolves selected elk over deer (Kunkel 1997). Cougars may have selected deer over elk because elk are at the upper limit size class of prey that can be killed by cougars. Karanth and Sunquist (1995) suggested that antipredator behavior, rather than size, may be a more important defense against ambush predators. Cougars may have greater difficulty surprising prey like elk that form groups to detect and avoid predators. The more closed habitats preferred by deer over elk during winter in our study area (Jenkins and Wright 1988) probably makes deer more vulnerable than elk to cougar predation (Kunkel 1997).

Wolf hunting success is influenced less by habitat features than is cougar hunting success (Mech 1970, Seidensticker et al. 1973, Kunkel 1997). As a result, differential prey selection between wolves and cougars also may be more evident in landscapes with greater habitat heterogeneity or in more open habitats than are present in our study area. Williams et al. (1995) speculated that vulnerability of mule deer, white-tailed deer, and elk to cougars on the Rocky Mountain front varied due to differential habitat use among seasons by these species. Similarly, prey selection and predator diet overlap may vary among landscapes (Christensen and Persson 1993).

Winter severity also may play a role in the amount of diet overlap between cougars and wolves. During more severe winters, deer are more concentrated in winter ranges (Jenkins and Wright 1988, Fuller 1991), which may result in greater wolf and cougar spatial overlap (T. K. Ruth, unpublished data). Relative vulnerability of cervids changes with differences in winter severity and thus may affect prey selection (Dale et al. 1995, Mech et al. 1995). The percentage of deer in wolf diets was positively correlated with annual total winter snow depths in our study area (Kunkel 1997).

Competition

Niche relations between species may be measured based on several parameters including activity patterns, space use, habitat use, and dietary overlap. If we assume prey is the limiting resource for large carnivores (Fuller 1989, but see Lindzey et al. 1994), then dietary overlap may be the most useful parameter to assess niche overlap. However, dietary overlap alone does not indicate the degree of competition (Lawlor 1980). Nevertheless, our observations of kleptoparasitism by wolves on cougar kills, direct killing of cougars by wolves (Boyd and Neale 1992; T. K. Ruth, unpublished data), and an apparent predator-related decline in the deer and elk population (Kunkel 1997) argue for exploitative and interference competition between cougars and wolves.

Competition between wolves and cougars has not yet resulted in significant partitioning of prey species in our study area. A partial explanation may be the large amount of prey biomass available. Gross estimates place the ungulate biomass index per wolf (Fuller 1989) in our study area among the highest measured in North America (250:1; K. E. Kunkel, unpublished data). As the biomass of prey declines, cougar prey selection may change as a result of competition with wolves. Strong directional selection during lean periods might result in adaptations that allow a species relatively exclusive use of a resource (Schoener 1982). Bobcat (*Lynx rufus*) diets in Maine may have shifted 10 years after colonization by coyotes (*Canis latrans*; Litvatis and Harrison 1989). Iriarte et al. (1990) speculated that prey selection by cougars in the Americas is influenced by competition resulting from evolution with sympatric jaguars (*Felis onca*).

At present, it seems unlikely that interference competition has resulted in a decline in the cougar population. Only 2 of 40 radiotagged cougars have been killed by wolves (T. K. Ruth, unpublished data), and adult cougars can readily escape wolf predation by climbing trees (Cypher 1993; T. K. Ruth, unpublished data). Additionally, we did not find any spatial displacement of cougars by wolves. However, 6 radiotagged cougars have died of starvation (T. K. Ruth, unpublished data). Starvation could result from exploitation competition or the overall prey population decline that is also affecting wolves (Kunkel 1997). If wolf consumption rates at cougar kills are significant, cougars may be forced to increase their kill rate as the wolf population continues to expand. Creel and Creel (1996) reported that wild dogs fare poorly where the percentage of dog kills fed on by hyenas (*Crocuta crocuta*) exceeded 60%. They also suggested that the highly overlapping diets of dogs and hyenas and resulting exploitation competition explained the negative correlation between densities of dogs and hyenas. Based on distribution of kills, we observed no evidence of this in wolves and cougars. As prey populations decline, however, this relation may change, and the carrying capacity for cougars may decline.

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