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SEASONAL RESOURCE USE AMONG MOUNTAIN LIONS, BOBCATS, AND COYOTES

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ABSTRACT.—Use of prey, and topographic and habitat features by mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in central Idaho was investigated to determine how syntopic carnivores coexist where resource use may overlap. There were significant differences in use of elevation, forest types, terrain, overstory density, and exposure by these predators during summer. Despite morphological and behavioral differences permitting these predators to partition resources, resource use overlapped during winter when snow confined prey and predators to lower elevations. Overlap in their diets was significant during winter resulting in mountain lions killing bobcats and coyotes while defending or usurping food caches.

Mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) occur together throughout much of western North America (Chapman and Feldhamer, 1982). Studies of syntopic bobcat and coyote populations show similar use of habitats and prey by these predators (Litvaitis and Harrison, 1989; Major and Sherburne, 1987; Witmer and DeCalesta, 1986) and their diets are similar to that of mountain lions (Ackerman et al., 1984; Hornocker, 1970; Leopold and Krausman, 1986; Young, 1958). We examined seasonal use of habitats and prey by mountain lions, bobcats, and coyotes in central Idaho to determine how these carnivores coexist where resource use may overlap. Information on resource use is needed for understanding community structure within an assemblage of large predators (Rosenzweig, 1966).

STUDY AREA AND METHODS

The study was conducted during 1980–1985 in a 1,500-km² area on the Big Creek drainage in the center of the Frank Church–River of No Return Wilderness, Idaho (45°N, 115°W). Elevations ranged from 1,036 to 3,048 m. Mean annual precipitation was 65 cm at 1,500 m elevation and snow depths exceeded 1 m at 1,500 m elevation during November–April. Mean temperature was –7°C during January and 18°C during August (United States Department of Commerce, 1988). Douglas fir (*Pseudotsuga menziesii*) associations dominated the lower elevations and subalpine fir (*Abies lasiocarpa*) and white bark pine (*Pinus albicaulis*) associations occurred at elevations above 1,500 m (Steel et al., 1981). Coyotes, bobcats, mountain lions, and black bears (*Ursus americanus*) were the major large carnivores in the area.

Because of marked differences in climate within the study area, we compared the diets and habitat use of mountain lions, bobcats, and coyotes between seasons. We identified summer as 1 May–31 October (when snow was absent below 1,500 m) and winter as 1 December–31 March (when snow was present below 1,500 m). Observations made in April and November were not analyzed because these were seasonal transition months.

Coyotes, captured in padded leghold traps, bobcats, captured in box traps, and mountain lions, captured with the aid of trail hounds, were immobilized with 22 mg of ketamine hydrochloride/kg of estimated body mass. Animals, fitted with radio-transmitter collars, were located from the ground at 1–5-day intervals and by aerial telemetry every 7–15 days. We approached within 500 m of animals and used triangulation to determine ground telemetry locations (Koehler and Hornocker, 1989). For each animal we recorded location according to the Universal Transverse Mercator coordinates from 7.5-minute topographic maps of the United States Geological Survey. Descriptions of topographic and habitat features for sites at which animals were located included elevation, exposure, nonrocky (estimates of ≤25% rocky terrain or bluffs) or rocky terrain (estimates of >25% rocky terrain or bluffs), and open (based on estimated distance ≥50 m between tree stems) or timbered (estimated distance <50 m between tree stems). We also identified sites as mesic forest types that included riparian, Douglas fir–ninebark (*Physocarpus malvaceus*), Douglas fir–pinegrass (*Calamagrostis rubescens*), Douglas fir–arnica (*Arnica cordifolia*) associations; xeric forest types, Douglas fir–mountain mahogany (*Cercocarpus ledifolius*) and Douglas fir–wheatgrass (*Agropyron spicatum*) associations; or alpine that included subalpine fir and white bark pine–whortle berry (*Vaccinium scoparium*) associations.

We used chi-square analysis to test for differential use of forest types, overstory density, exposure, and

terrain among species and between seasons. Student's *t* test, analysis of variance, and Tukey multiple-comparison tests (Zar, 1984) were used to determine interspecific and seasonal differences in use of elevations by these predators.

Food habits of these predators were determined from inspection of ungulate carcasses and calculations of the frequency of occurrence of items found in feces. Presence of tracks or scrapes and size and form of feces were used to identify the species depositing feces. Prey items within feces were identified by comparison to a reference collection. Identity of predators that killed ungulates was determined from presence of tracks or scrapes near carcasses, size, depth, and spacing of canine punctures on carcasses, location of hemorrhage on carcasses, and whether carcasses were covered with snow, dirt, grass, or sticks. If it appeared the ungulate died from disease, accident, or from unknown causes, we did not consider the death predator related. If the cause of death of the ungulate was not conclusive, but a predator was visiting the carcass, the visiting carnivore was considered scavenging.

RESULTS

We obtained 187 radiotelemetry locations (range 1–46 locations animal⁻¹ season⁻¹) from five male and eight female adult coyotes, 594 locations (2–62 locations animal⁻¹ season⁻¹) from 14 male and 16 female bobcats, and 228 locations (1–44 locations animal⁻¹ season⁻¹) from four male and 11 female adult mountain lions. The greater number of captures and locations obtained for bobcats reflected the greater effort devoted toward capturing bobcats (Koehler and Hornocker, 1989).

During winter, coyotes used areas significantly ($t = -4.8$, $P < 0.001$) lower in elevation ($\bar{X} \pm SD = 1,347 \pm 146$ m) than in summer (1,503 \pm 278 m), but there was no seasonal shift in their selection for topographic or habitat features. Coyotes used open stands and all forest types (except alpine) situated on south-southwest exposures during winter and summer (Table 1).

For bobcats there also were significant differences ($t = -26.1$, $P < 0.001$) in use of elevations between winter (1,365 \pm 200 m) and summer (1,852 \pm 301 m). Unlike coyotes, there were significant differences between seasons in use of forest types by bobcats ($\chi^2 = 120.4$, $d.f. = 3$, $P < 0.001$), stand density ($\chi^2 = 145.8$, $d.f. = 1$, $P < 0.001$), terrain ($\chi^2 = 47.4$, $d.f. = 1$, $P < 0.001$), and exposure ($\chi^2 = 59.7$, $d.f. = 1$, $P < 0.001$). Bobcats used Douglas fir–mountain mahogany types, open areas, and rocky terrain more frequently during winter than summer. They also concentrated their activities on south-southwest exposures during winter, whereas all exposures were used in almost equal proportions during summer (Table 1).

Mountain lions also used topographic and habitat features differently between seasons. They occupied lower elevations during winter (1,479 \pm 166 m) than in summer (2,001 \pm 248 m, $t = -14.8$, $P < 0.001$). There also were differences in their use of forest habitat types ($\chi^2 = 70.8$, $d.f. = 3$, $P < 0.001$), stand density ($\chi^2 = 20.7$, $d.f. = 1$, $P < 0.001$), and terrain types ($\chi^2 = 10.8$, $d.f. = 1$, $P < 0.001$). Forty-three percent of locations of mountain lions were in Douglas fir–wheatgrass habitat types during winter, but 46% were among mesic areas in summer. Mountain lions favored timbered areas with nonrocky terrain in summer, but they used open areas with rocky terrain on south-southwest exposures during winter (Table 1).

During summer, these three predators differed in their use of elevations ($F = 79.3$, $d.f. = 2, 517$, $P < 0.001$), with coyotes using lower elevations (1,503 m) than bobcats (1,852 m) or mountain lions (2,001 m). Bobcats' use of exposure differed significantly from that of coyotes ($\chi^2 = 19.2$, $d.f. = 1$, $P < 0.001$), with coyotes and mountain lions tending to favor south-southwest exposures during summer. Use of open areas by coyotes differed from that of the felids, which used timbered areas (coyotes' and bobcats' use of stand density, $\chi^2 = 60.4$, $d.f. = 1$, $P < 0.001$; coyotes and mountain lions, $\chi^2 = 32.0$, $d.f. = 1$, $P < 0.001$). In addition, there were significant differences in use of forest habitat types during summer between coyotes and bobcats ($\chi^2 = 24.9$, $d.f. = 3$, $P < 0.001$), coyotes and mountain lions ($\chi^2 = 42.3$, $d.f. = 3$, $P < 0.001$), and bobcats and mountain lions ($\chi^2 = 17.9$, $d.f. = 3$, $P < 0.001$).

Compared to summer, there was greater overlap in use of topographical and habitat features during winter. All predators concentrated their activities on the relatively snow-free south-southwest exposures (ca. 60% of use by each predator), although mountain lions used higher elevations than either bobcats or coyotes ($F = 45.9$, $d.f. = 2, 779$, $P < 0.001$, Tukey test). Coyotes

TABLE 1.—Percent of radiotelemetry locations for mountain lions, bobcats, and coyotes among forest types, stand densities, terrain types, and exposures during winter (December–March) and summer (May–October) in the Frank Church–River of No Return Wilderness, Idaho, 1980–1985.

Habitat variable	Winter			Summer		
	Mountain lion	Bobcat	Coyote	Mountain lion	Bobcat	Coyote
Forest cover type						
Mesic ^a	26	18	29	46	35	20
Douglas fir–mountain mahogany	31	50	34	4	11	27
Douglas fir–wheatgrass	43	32	37	22	44	50
Alpine ^b				28	10	3
Stand density (distance between trees)						
Open (≥ 50 m)	55	73	61		22	66
Timbered (< 50 m)	45	27	39	100	78	34
Terrain (percent rock and bluffs)						
Nonrocky ($\leq 25\%$)	33	21	43	67	46	41
Rocky ($> 25\%$)	67	79	57	33	54	59
Exposure						
North-northeast	8	11	16	19	18	15
East-southeast	19	15	12	26	22	22
South-southwest	62	61	59	42	31	52
West-northwest	12	13	13	13	29	13

^a Riparian, Douglas fir–ninebark, Douglas fir–pinegrass, Douglas fir–arnica.

^b Subalpine fir and whitebark pine–whortleberry.

and mountain lions tended to use elevations differently, but there were no statistical differences in their selection for topographic and habitat features, indicating greater resource overlap during winter by coyotes and mountain lions. Although coyotes and bobcats both used open stands at lower elevations during winter, there were significant differences in their selection for terrain ($\chi^2 = 14.9$, $d.f. = 1$, $P < 0.001$) and forest habitat types ($\chi^2 = 7.1$, $d.f. = 3$, $P = 0.03$).

For bobcats and mountain lions during winter, significant differences existed in their use of forest habitat types ($\chi^2 = 17.4$, $d.f. = 3$, $P < 0.001$), terrain ($\chi^2 = 6.2$, $d.f. = 1$, $P = 0.01$), and stand density ($\chi^2 = 14.7$, $d.f. = 1$, $P < 0.001$). This suggests partitioning of habitats among felids, with bobcats using open rocky Douglas fir–mountain mahogany types and mountain lions using open and timbered stands of Douglas fir–wheatgrass.

Although the three carnivores used the same prey, the proportion of items in their diets differed. Small mammals frequently were consumed by bobcats and coyotes (Table 2), but were eaten infrequently by mountain lions (Hornocker, 1970). In contrast, ungulates frequently occurred in the diet of mountain lions (70% of 198 mountain lion feces contained deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) remains—Hornocker, 1970) and less frequently in the diet of bobcats and coyotes (Table 2). Although mountain lion feces were not examined during this study, the ratio of 1.2 elk to one deer killed by mountain lions during the present study, augmented by the data of Hornocker (1970), denote similarity of diets. Inspection of ungulate carcasses indicated these predators differed in hunting and scavenging strategies. Mountain lions were the major predators of elk, killing 70% of the 26 elk examined, whereas coyotes killed one calf, and bobcats killed no elk. All three carnivores preyed on deer, but coyotes killed 34%, mountain lions 22%, and bobcats 10% of 67 deer examined. Coyotes scavenged most frequently, feeding on 79% of the 100 deer, elk, and bighorn sheep (*Ovis canadensis*) examined, whereas mountain lions scavenged on 4% and bobcats on 5% of carcasses.

DISCUSSION

Although mountain lions, bobcats, and coyotes overlapped in their use of space and used similar prey, morphological and behavioral differences permitted partitioning of prey and habitat re-

TABLE 2.—Frequency (%) of prey identified in coyote and bobcat feces collected in the Frank Church–River of No Return Wilderness, Idaho, 1982–1985.

Prey	Summer (April–October)		Winter (November–March)	
	Coyote	Bobcat	Coyote	Bobcat
<i>n</i>	30	25	143	135
<i>Microtus</i> sp.	46.7	40.0	37.8	65.2
<i>Peromyscus maniculatus</i>	6.6	4.0	2.8	3.7
Unknown mice-voles	10.0	12.0	6.3	10.4
<i>Thomomys talpoides</i>		4.0		
<i>Neotoma cinerea</i>	23.3	8.0	6.3	7.4
<i>Tamias</i> sp.	3.3			0.7
<i>Sylvilagus nuttallii</i>	10.0	36.0	6.3	1.5
<i>Spermophilus columbianus</i>	23.3	32.0		
<i>Tamiasciurus hudsonicus</i>	3.3	4.0		2.2
<i>Sorex</i> sp.				0.7
<i>Odocoileus hemionus</i>	40.0		51.0	26.7
<i>Ovis canadensis</i>	10.0	4.0	22.4	15.6
<i>Cervus elaphus</i>	3.3		4.2	
Unknown ungulates	6.6		2.8	1.5
Reptiles	10.0		0.7	
Birds	10.0	12.0	2.0	3.7
Insects	10.0			
Grass	6.6		1.4	

sources. Bobcats and mountain lions, commonly associated with areas in which cover for stalking is present (Koehler and Hornocker, 1989; Logan and Irwin, 1985; Seidensticker et al., 1973), occupied timbered and rocky terrain in the Frank Church–River of No Return Wilderness. Use of open areas and a variety of forest types by coyotes during this study was consistent with observations of their wide distribution and use of open habitats (Gese et al., 1988a; Gier, 1975; Litvaitis and Shaw, 1980). Differences in use of habitats by the stalking felids and coursing canids were expected from these morphologically different families (Eisenberg, 1986).

Morphological and behavioral differences explained the more selective use of prey and habitats by bobcats than mountain lions during winter. Bobcats preyed on voles (Arvicolinae) on snow-free xeric sites (Koehler and Hornocker, 1989) and mountain lions hunted the more widely distributed elk and deer (Hornocker, 1970; Seidensticker et al., 1973). Mountain lions, because of their larger body size, were better able than other predators to negotiate greater snow depths and exploit higher elevations and mesic habitats where snow was deeper. Bobcats used the snow-free south-southwest exposures at lower elevations because their small feet and small body size made it difficult for them to negotiate deep snow found at higher elevations (Litvaitis et al., 1986; McCord, 1974; Parker et al., 1983). Differences in body size also may explain the differences in diet of these felids (Rosenzweig, 1966). Bobcats, because of their small body size, used small-sized prey, whereas mountain lions killed predominantly ungulates.

Coyotes' use of habitats and prey overlapped that of both felids. Coyotes used xeric sites where, like bobcats, they hunted voles and used mesic areas, like mountain lions, probably in search of ungulates as prey and carrion. Ungulates are vulnerable to predation by coyotes in deep snow or when chased onto frozen streams (Gese et al., 1988b; Ozoga and Harger, 1966). Deer and elk may seek riparian and mesic habitats with greater density of overstory for security and thermal cover (Jenkins and Wright, 1988); this may explain the attraction to such sites by coyotes. Cursorial adaptations and social behavior may permit coyotes to negotiate the deep snow on mesic sites (Gese et al., 1988b).

Keen sense of smell and pack formation also may enable coyotes to prey and scavenge for ungulates and to defend food (Beckoff and Wells, 1980; Bowen, 1981; Gese et al., 1988b). Groups of coyotes often consumed and scattered deer or elk carcasses into caches in <24 h, thus reducing

opportunities for scavenging from other carnivores (Bowen, 1981; Lamprecht, 1978). Of 24 ungulates killed by coyotes, none was visited by bobcats or mountain lions, whereas three of seven bobcat kills were visited by coyotes and mountain lions, and 13 of 33 kills of mountain lions were visited by coyotes and bobcats.

During winter, greater overlap in use of habitats and prey may be expected, and interspecific contacts may increase as these predators and prey congregate at lower elevations. Increased contact and overlap in resource use among these predators was shown by four bobcats and two coyotes killed by mountain lions near feeding sites during winter. The proximity of these kills to feeding sites and the fact that five bobcats and two coyotes were left intact suggests that these predators were killed by mountain lions defending or usurping a food cache. We observed mountain lions feeding on deer killed by bobcats. In Montana, Boyd and O'Gara (1985) reported mountain lions killing and not consuming coyotes apparently to protect food caches. Mortalities caused by mountain lions were significant, accounting for five of eight deaths of bobcats and three of seven deaths of coyotes.

Carnivores can coexist where resources are partitioned (Rosenzweig, 1966). Partitioning of resources and structure of predator communities are influenced, in part, by an interaction of environmental factors, and species behavior and morphology (Hayward and Garton, 1988; Jenkins and Wright, 1988; Rosenzweig, 1966; Schoener, 1986; Wiens, 1984). Behavioral and morphological differences permitted mountain lions, bobcats, and coyotes to partition use of habitats and prey, but seasons also influenced the selection and degree of overlap of resource use.

During winter when resources were confined, overlap in resource use among mountain lions, bobcats, and coyotes was significant and mountain lions killed bobcats and coyotes while defending or usurping food caches. Interference competition (when aggression by the dominant species denies subordinates access to the needed resources—Case and Gilpin, 1974; Litvaitis and Harrison, 1989) may influence the selection of habitats by subordinate species (Case and Gilpin, 1974). Interference competition by coyotes was shown to influence red fox (*Vulpes vulpes*) use of habitat and space (Dekker, 1983; Harrison et al., 1989; Major and Sherburne, 1987; Sargeant and Allen, 1989; Sargeant et al., 1987; Voigt and Earle, 1983). In a similar manner, interference competition, together with environmental factors, and species behavior and morphology, may influence use of resources by bobcats and coyotes as well as influence the niche relationships and structure of the carnivore community in the Frank Church–River of No Return Wilderness.

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