Wendy M. Arjo[1] and **Daniel H. Pletscher,** Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana, 59812

Coyote and Wolf Habitat Use in Northwestern Montana

Abstract

Being a habitat generalist is an adaptation strategy that has allowed the coyote to expand its range. As wolves reestablish, or are reintroduced, resident populations of coyotes may change habitat use. We compared habitat use between coyotes and wolves in Glacier National Park after successful recolonization by wolves. Two wolf packs and nine coyotes were monitored from June 1994 through June 1997 to determine habitat use in northwestern Montana. Wolves used habitat types within their home ranges in proportion to availability during the winter, but not the summer when more open areas and burned forest were used. Most coyotes used habitat types within their home ranges in proportion to availability in summer and winter. However, two coyotes used open areas more during the summer and lowland forests areas more during the winter. Coyotes may use open habitats to avoid encounters with predators other than wolves (i.e., cougars), and for access to small mammals during the summer. In addition, coyotes used areas closer to roads than wolves, and used NE-NW aspects more frequently while wolves occupied SE-SW and SW-NW aspects. Although habitat use was similar between canids, coexistence of coyotes and wolves in the Glacier National Park area may be facilitated through differential use of topographic characteristics (i.e., slope, aspect, and areas near roads).

Introduction

Coyotes (*Canis latrans*) are one of the most widely distributed carnivores in North America (Chapman and Feldhammer 1982). Historically adapted to the arid plains of the West and Midwest (Young and Jackson 1951), coyotes expanded their range into forested habitats of eastern North America early in the 20th century. The expansion of the coyote distribution is believed due, in part, to the extirpation of the wolf (*C. lupus*) (Young and Jackson 1951, Mech 1970). Coyotes now occupy a variety of habitats; however, even in the eastern expansion, semiagricultural areas support higher coyote densities than heavily forested areas (Hilton 1978). Although forested or heavy brush areas are often preferred for denning (Andrews and Boggess 1978, Litvaitis and Shaw 1980), preference for habitats is usually prey-related (Litvaitis and Shaw 1980, Andelt and Andelt 1981, Gese et al. 1988).

Wolves historically occupied a variety of habitats with the exception of the arid deserts and tropical rain forest (Mech 1970); however, current populations are restricted to forested areas of Canada and northern portions of the contiguous United States and a variety of habitats in Alaska. Fritts et al. (1994) and Boyd-Hager (1997) suggest that the two most critical habitat components for wolves are: 1) freedom from excessive human persecution; 2) abundant supply of ungulates. Apart from availability of prey, researchers have documented more specific habitat requirements during parturition and pup rearing. Elevated forested areas near water sources for denning and meadow or semi-open to partially treed areas for rendezvous sites (Joslin 1967, Mech 1970, Ballard and Dau 1983, Ream et al. 1989, Matteson 1992) are preferred habitats during this period.

Abundance of prey (Ozoga and Harger 1966, Litvaitis and Shaw 1980, Andelt and Andelt 1981, Reichel 1991, Holzman et al. 1992), interspecific interactions (Major and Sherburne 1987, Harrison et al. 1989, Sargeant et al. 1987), ease of travel (Haplin and Bissonette 1988, Theberge and Wedeles 1989, Murray and Boutin 1991) and energy requirements (McNab 1963) are a few factors that can influence habitat use. Habitat provides necessary requirements for species' survival; however, some species may be excluded from available habitat by a more competitive species (Case and Gilpin 1974). Chances for interspecific interactions between coyotes and other predators is high within the North Fork of the Flathead area given the number of predators and variety of niches

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[1]Author to whom correspondence should be addressed. Current address: USDA/Animal and Plant Health Inspection Service/Wildlife Service/National Wildlife Research Center, 9730-B Lathrop Industrial Dr. SW, Olympia, Washington, 98512.
E-mail: wendy.m.arjo@aphis.usda.gov

filled by predators. Wolf populations steadily increased in the area until 1993 when they appeared to peak and remained stable at 25-30 animals (Pletscher et al. 1997), while coyote populations appeared to decline (Arjo and Pletscher 1999). In addition, cougar (*Puma concolor*) densities in the North Fork were 70 cougars/1,000 km², and black bear (*U. americanus*) densities were 200 bears/1,000 km². Grizzly bear (*Ursus arctos*), densities estimated from the northern portion of the study area in Canada were 64 bears/1,000 km². Additional predators affect abundance and availability of prey for coyotes. Coyotes exploit areas with higher prey densities, often changing their use of habitats to accommodate food requirements (Andelt and Andelt 1981, Roy and Dorrance 1985).

Shifts in habitat use by less competitive species can occur as large carnivores recolonize or are reintroduced into areas where other carnivore species are established. Recolonizing wolves may exclude coyotes from certain habitats, or force coyotes into areas closer to human habitation, which may increase coyote-human or coyote-livestock interactions. Differential use of habitat types or topographic characteristics is one method of spatial partitioning that allows for coexistence of congeneric species. At a landscape scale in the Central Rocky Mountains, Boyd-Hager (1997) found that wolves selected areas closer to roads, which was highly correlated with elevation, distance to water, and prey availability. Wolf survival varies in response to road density (Thiel 1985, Mech et al. 1988, Mech 1989, Mladenoff et al. 1995), with usually a decrease in survival with an increase in road density (Boyd-Hager 1997). Wolves can therefore restrict coyote use of topographic features like roads for ease of travel by their presence.

Several researchers have documented coyote (Ozoga and Harger 1966, Andelt and Andelt 1981, Roy and Dorrance 1985, Witmer and deCalesta 1986, Gese et al. 1988) and wolf (Fritts and Mech 1981, Mladenoff et al. 1995) habitat use, but not in areas where the two species occur sympatrically. In addition, Carbyn (1982), Paquet (1989), and Thurber et al. (1992) documented the coexistence and interaction between wolves and coyotes but did not discuss differential habitat use. Johnson et al. (1996) emphasized the need in carnivore research to understand how species select resources within their home range during differ-

ent time periods and within different guild assemblages. Experimental removal, addition, or manipulation of predator populations is often difficult but provides the most reliable information for understanding the effects of one predator on another. Recolonization of the North Fork area near Glacier National Park, Montana, by wolves in the 1980s (Ream et al. 1991) offered a natural experiment to estimate the effects wolves may have on coyote habitat selection.

We examined habitat use by wolves and coyotes along the North Fork of the Flathead River where these species are now sympatric. Our objectives were to determine: 1) second and third order habitat selection by coyotes and wolves; 2) if wolves and coyotes partitioned use of habitat features; and 3) measures of habitat overlap.

Methods

We conducted this study along the North Fork of the Flathead River drainage in northwestern Montana from 1994-1997. The 3,000 km² study area extends from just north of the Montana-Canadian border south to the Apgar Mountains, and is bounded by the Whitefish divide on the west and the Livingston Range on the east. The valley bottom is 4-10 km wide and ranges in elevation from 1,374 m above sea level in the north to 1,024 m in the south. Lands west of the North Fork River are a conglomerate of private, National, and State forests. East of the river is Glacier National Park (GNP).

The dominant cover in the North Fork is lodgepole pine (*Pinus contorta*), although western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*), communities are also present in the valley. Riparian areas are dominated by spruce (*Picea* spp.) and black cottonwood (*Populus trichocarpa*) (On and Shaw 1979). Over 15,400 ha in the middle of the study area near Polebridge was burned in 1988. Maximum average daily temperatures range from -2.2°C (January) to 27.3°C (July), and average minimum daily temperatures range from -13.2°C (January) to 5.0°C (July) for 1994-1997 (Polebridge weather station). Snow usually remains on the ground from mid-November through mid-April.

The North Fork study area contains several large predator species including coyotes, wolves, grizzly bears, black bears, wolverines (*Gulo gulo*),

and cougars. Bobcats (*Lynx rufus*), fisher (*Martes pennanti*), marten (*M. americana*), and lynx (*L. canadensis*) represent smaller carnivores in the area. Large prey species include elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Potential small mammal prey species include snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), mountain cottontail (*Sylvilagus nuttalli*), red squirrel (*Tamiasciurus hudsonicus*), Columbian ground squirrel (*Spermophilus columbianus*), and various vole and mice species.

Capture and Monitoring

Wolves were captured and handled according to Mech (1974) and Ream et al. (1991) from May through June 1994-1996 and September through October of 1994. We attempted to maintain at least two radio-collared wolves in each of the two packs. Coyotes were captured in double-staked, padded No. 3 soft-catch foot-hold traps in early spring (May-June) and fall (September-October) 1994-1996. We determined sex and measured, weighed, and initially aged coyotes from tooth wear (Gier 1968). We fitted coyotes ≥ 6 mo old with a mortality-sensing radio.

We located canids ≥ 2 times a week from the ground and at least once a month from the air from July 1994 - June 1997. Canids were tracked throughout the day and for 24 hr periods to delineate home ranges (Laundré and Keller 1984). At least two bearings, ≤ 20 min apart, were obtained using a hand-held H-antenna. We plotted each location on a 1:24,000 U.S. Geological Survey topography map using Universal Transverse Mercator grid system. We recalculated canid locations using the program Locate II (Truno, Nova Scotia, Canada) to incorporate bearing error.

We estimated composite canid home ranges (home range estimated from locations obtained during the entire period an animal transmitted) for each individual coyote and each wolf pack using the adaptive kernel method (Worton 1989) in the program CALHOME (Kie 1992). Following Shivik et al. (1996), we determined the maximum probability contour for a canid's home range by graphing the area for each home range against each probability. The maximum probability for each canid home range was determined to be the probability where the home range size reached an asymptote. Maximum-probability contours for all canids were averaged and then used for our home range estimates. From this analysis, we determined that the 94% contour best described both wolf and coyote home ranges.

Habitat Use

We used vegetation types classified by Montana gap analysis from the Montana Cooperative Wildlife Research Unit Spatial Analysis Laboratory at the University of Montana (Redmond 1996). Twenty-six different vegetation types were distinguished in the gap analysis; however, we condensed these vegetation types into six categories based on Kunkel (1997) for our analyses (Table 1). Habitat categories with $\leq 5\%$ locations were pooled with other similar habitats for analysis. Second and third order habitat selection (Johnson 1980) were used in habitat analyses: second or-

TABLE 1. Vegetation classification from gap analysis for the North Fork of the Flathead River study area in northwestern Montana (modified from Kunkel 1997).

Habitat name	Associated habitat categories
Open/Barren	Low/moderate and moderate/high grass, parklands, meadows, mixed mesic shrub, alpine meadows, altered herbaceous, rock, barren site, snowfields, and ice
Burned timber	Area burned in 1988 fire (Red Bench Fire)
Mixed conifer stands	Douglas-fir, lodgepole pine, mixed broadleaf, mixed broadleaf and conifer, and Douglas-fir/lodgepole pine
Upland conifer	Mixed subalpine fir, limber pine (*Pinus flexilis*), grand fir (*A. grandis*), upland spruce (*Picea engelmannii*), and whitebark pine (*P. albicaulis*)
Mesic forest	Mixed mesic forest, western larch, western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*)
Lowland conifer	Ponderosa pine and mixed xeric forest

der compared individual canid home ranges (use) versus availability within the study area, while third order compared individual canid locations (use) versus availability within individual home range.

We used a 100% minimum convex polygon (MCP) that encompassed all coyote locations to delineate availability of habitat types within the study area for the second order analyses (Poole et al. 1996). This method delineated a maximum area used by the coyotes by encompassing all location points. The same method was used to determine habitat availability for wolves using all wolf locations. Habitat types within each individual canid composite home range and in the study area were determined using the Geographic Information System programs ARCINFO and ARCVIEW. To test whether coyotes and wolves used habitats in proportion to their availability considering all habitats simultaneously, we used independent Chi-square tests and Bonferroni confidence intervals (Neu et al.1974, Alldredge and Ratti 1986). This measure was appropriate given that habitat availability was measured, not estimated (the method allows for unequal variance between habitats) (Alldredge and Ratti 1992). To avoid spatial dependence of locations, we used only one animal from a mated pair. Mated pairs are biologically dependent upon one another and therefore should not be considered independent locations (Millspaugh et al. 1998). A similar comparison was made between use of habitat types by the two wolf packs to that available in the wolf 100% MCP. We determined overlap of habitat use between coyotes and wolves using Horn's (1966) index of overlap $C_\lambda = 2\,Sx_iy_i / (Sx_i^2 + Sy_i^2)$; where x_i = proportion of habitats in coyote ranges, and y_i = proportion of habitats in wolf ranges. Complete overlap of habitats would result in a maximum value $C_\lambda = 1.0$.

We used coyotes with ≥ 20 relocations during both summer and winter and both wolf packs in the third order analysis to minimize Type II error (Alldredge and Ratti 1986). Expected values were based on the proportion of each habitat type in the individual canid's home range multiplied by the number of locations for that canid. We compared third order habitat use during winter (October 1 - April 14) and summer (April 15 - September 30) using chi-square goodness of fit (Neu et al. 1974).

We compared the distance to a road or water source from coyote locations to wolf locations for both seasons. Only primary and secondary roads accessible throughout the winter were used in the road comparison. We compared elevation, slope, and aspect to test whether the use of topographic characteristics differed between species. Differences in elevation for each canid location were tested using a t-test. We classified topography into five aspect classes (flat, 46° to 135°, 136° to 225°, 226° to 315°, and 316° to 45°) and four slope classes (no slope, 1° to 10°, 11° to 20°, and > 20°). We used a chi-square contingency table to test for differences in topography between wolf and coyote locations. A residual z-test (Haberman 1973) was used to determine which cells contributed the most to the chi-square analyses. Significance was inferred at $P \leq 0.05$ for all tests.

Results

Radio Tracking

We captured and collared 18 coyotes, 9 males and 9 females, and 5 adult wolves in the two wolf packs. We also monitored 5 wolves previously collared in the two packs. Only coyote and wolf locations with ≤ 2 km^2 error polygon were used in the home range analyses and locations with $\leq$ 0.25 km^2 error were used in the habitat analyses. Composite home range size for 4 male coyotes averaged 99.4 km^2 and for 5 females averaged 126.7 km^2. The South Camas Pack wolves had a composite home range of 686.4 km^2, and the North Camas Pack wolves 477.0 km^2.

Habitat Use

For the second order resource selection analysis our available habitat area for coyotes was 831.9 km^2 and for wolves was 1,194.8 km^2. Five composite coyote home ranges and two composite wolf pack home ranges were compared to availability of the six habitat types. Four other coyotes were determined to be either the mate or pack member of a coyote used in the analyses. Nine other coyotes did not transmit long enough to define home ranges. Coyotes did not use habitats in proportion to availability ($P < 0.001$; Table 2). Open areas, burned areas, and lowland conifer forests were used more than expected, and mixed conifer and upland conifer forests were used less. Wolves did not use habitat types within the study

TABLE 2. Proportion of habitat used in home ranges by individual radio-collared coyotes (numbers) and wolf packs and proportion of area within the study area in northwestern Montana.

Canid identification	Open/Barren	Burned	Mixed conifer	Upland conifer	Mesic	Lowland conifer
5294	0.132	0	0.107	0.310	0.418	0.033
5194	0.035	0.391	0.052	0.055	0.460	0.007
0294	0.930	0	0.085	0.430	0.369	0.022
5395	0.012	0.821	0.026	0.008	0.131	0
0996	0.088	0	0.206	0.042	0.664	0
South Camas Pack	0.015	0.207	0.247	0.074	0.455	0.001
North Camas Pack	0.099	0.003	0.234	0.205	0.329	0.014
Porportion available to coyotes	0.045	0.139	0.183	0.273	0.355	0.005
Proportion available to wolves	0.088	0.103	0.249	0.226	0.328	0.007

area in proportion to availability ($P < 0.001$). Wolves used more mesic forests and less mixed conifer and lowland conifer forests than expected. Overlap of habitat use was high between wolves and coyotes ($C_\lambda = 0.94$) at the second order.

The third order analysis showed that three coyotes used habitats in proportion to availability within their respective home ranges. Two coyotes did not use each habitat in proportion to its availability within their home range ($P < 0.001$) in summer. A female coyote (5194) used less burned area than available and more open and lowland conifer forests; female 5294 used more open areas than was available. The same two coyotes used habitat differently from available in the winter (5194: $P = 0.002$; 5294: $P = 0.004$). These females used lowland forests more frequently than expected based on availability within their respective home ranges. Both wolf packs used habitat within their home ranges in proportion to availability in the winter, but differently in the summer ($P < 0.001$). The South Camas Pack used more open areas and less mixed conifer forests than available, whereas the North Camas Pack used more burned areas. Overlap of habitat use was high between the species in summer ($C_\lambda = 0.97$) and winter ($C_\lambda = 0.96$).

Coyotes were found closer to roads than wolves during winter ($P < 0.001$) and summer ($P < 0.001$; Table 3). Coyotes were closer to water sources in summer ($P = 0.04$) than wolves. Use of elevation was similar between canids in winter and summer. However, canids used different slope categories during summer ($P = 0.04$); coyotes used

no-aspect slopes (flat areas) more than wolves ($P = 0.013$). In the winter, slope use differed between the canids ($P = 0.005$) where coyotes again used relatively flat areas ($P = 0.003$) and wolves more areas with 11-20° of slope ($P = 0.014$). Aspects used by the canids also differed significantly in summer ($P < 0.001$) and winter ($P < 0.001$). Coyotes used flat ($P = 0.047$) and NE-SE aspect ($P < 0.001$) areas more in summer than did wolves. Wolves used SE-SW ($P = 0.002$) and SW-NW ($P = 0.003$) aspects more during summer than coyotes. Coyotes again used more NE-SE aspects in the winter ($P < 0.001$) and wolves more SE-SW ($P < 0.001$).

Discussion

Distribution and abundance of prey (Ozoga and Harger 1966, Litvaitis and Shaw 1980, Holzman et al. 1992) and prey preference, may affect seasonal habitat use by canids. For wolves, the ability to encounter, detect, and capture prey depends on habitat and spatial features (Kunkel and Pletscher 2001). Wolf home ranges encompassed more mesic forest habitat than expected based on availability within the study area (Table 2). This difference in use is likely related to the use of mesic forest for hunting routes in the North Fork (Kunkel and Pletscher 2001).

Individual pack differences were observed only in the summer when the South Camas Pack used more open areas, and the North Camas Pack used more burned areas. Den site and rendezvous sites used by wolves likely influenced use of open habitat in the summer. The South Camas Pack den at the

TABLE 3. Topographic characteristics used by coyotes and wolves in northwestern Montana during summer and winter. Average distance to roads and water and average elevation used by coyotes and wolf packs (m $\pm$ SE; n = number of telemetry locations).

	Summer		Winter	
	Coyote (n = 158)	Wolf (n = 111)	Coyote (n = 130)	Wolf (n = 92)
Roads	288.9 $\pm$ 44.8[a]	882.3 $\pm$ 117.4	246.5 $\pm$ 32.8[a]	1101.8 $\pm$ 169.0
Water	291.6 $\pm$ 20.8[b]	8.0 $\pm$ 27.9	282.7 $\pm$ 21.5	309.9 $\pm$ 34.2
Elevation	1174.6 $\pm$ 8.1	1171.0 $\pm$ 10.3	1172.5 $\pm$ 8.1	1176.2 $\pm$ 18.2

[a] $P < 0.001$
[b] $P < 0.05$

edge of a meadow system was consistently used every year. This open meadow area was used as a rendezvous site for the rest of the summer as the pups matured. We only documented one coyote denning in a meadow system during our study. Other studies have documented forest areas with greater cover as preferred denning areas for coyotes (Litvaitis and Shaw 1980, Gese et al. 1988).

The flexible nature of coyotes, observed in the differential use of habitats by individuals, allows this species to adapt to changes in its environment more readily than most predators. Coyote use of open areas is likely related to prey availability in the summer. Person and Hirth (1991) found that coyotes in Vermont preferred open habitats during the summer and fall, similar to our findings. Additionally, Reichel (1991) documented coyotes in Montana used riparian habitats where microtines were more plentiful. Coyotes may also be using these areas more to increase opportunist encounters with wolf kills. Deer use riparian areas for thermal cover and security (Jenkins and Wright 1988), and Kunkel and Pletscher (2001) found deer killed by wolves tend to be close to water. During the winter, small prey species are less accessible and, therefore, fewer prey species are available to coyotes (Litvaitis and Harrison 1989). Although large ungulate prey, which may increase prey biomass, often congregate at lower elevation during the winter (Koehler and Hornocker 1991), these prey species are not preyed upon by coyotes (Arjo et al. 2002). However, coyotes and wolves used similar habitats in winter and habitat overlap was high, which may be related to the increased use of scavenged ungulates by coyotes after wolves recolonized the area (Arjo et al. 2002).

Unlike most areas, the major cause of mortality of coyotes in North Fork was predation by wolves and cougars. Wolves dominate coyotes in encounters as noted by the killing of coyotes by wolves (Carbyn 1982, Paquet 1989, Arjo and Pletscher 1999). Three of the radio-collared coyotes in our study were killed by wolves, whereas cougars were responsible for the other six predator-caused mortalities. Four of the six cougar-killed coyotes were located in dense old-growth forests and the remaining two in mature larch stands. Unlike wolves, cougars are solitary animals. Coyotes spatially segregate themselves from wolves (Arjo and Pletscher 1999), but may have a difficult time spatially maintaining a home range away from cougars. Coyotes may prefer open areas (low canopy cover) to minimize cougar predation (Koehler and Hornocker 1991).

Coyotes and wolves used similar habitat types; however, at a finer spatial scale, these two species chose different topographic characteristics (Table 3). Singleton (1995) and Kunkel (1997) found that wolves traveled in areas with $\leq 15°$ slope, and Singleton (1995) found they used SW aspects for travel similar to our winter observations. Differential use of slope and aspect by predators may be related to prey availability. Cervids usually select slopes with shallow snow for winter ranges (Jenkins and Wright 1988, Bureau 1992, Rachael 1992, Langley 1993, Singleton 1995, Kunkel 1997). Kunkel and Pletscher (2001) documented that areas with greater slope and less hiding cover increased the probability that the site was located along wolf hunting routes. Coyotes, on the other hand, used NE-NW aspects in both summer and winter. Coyotes selected NE-NW exposures and used significantly less the SE-SW and SW-NW exposures used by wolves. Coyotes used NE-NW aspects in both the summer and winter, possibly for access to areas with high murid production (Todd et al. 1981) and to reduce competition

with wolves. This differential use of aspect and slopes, especially in winter when spatial overlap was greatest, may reduce encounters with wolves while maintaining high habitat overlap. In addition, coyotes temporally partitioned their use of habitat during winter in this study area (Arjo and Pletscher 1999) as an additional mechanism for coyotes to avoid encounters with wolves while scavenging.

Humans can also influence where wolves establish home ranges (Mladenoff et al. 1995). Recolonizing wolves may force coyotes into habitats closer to human habitation, which may be less desirable due to human persecution in many areas. Humans were the leading cause of wolf mortality in this recolonizing population, and 75% of the human-caused mortality occurred $\leq$ 250 m from roads (Boyd-Hager 1997). Coyotes can tolerate anthropogenic effects better than wolves, and are often attracted to open roads (Thurber et al. 1992). In addition, coyotes may use areas closer to roads to avoid encounters with wolves.

Catholic food habits, the ability to associate with humans, and the ability to function in a wide range of habitats have allowed the coyote to expand its range (Litvaitis 1992). As wolves reestablish, or are reintroduced, resident populations of coyotes may change habitat use. Interspecific interactions and prey availability appears to influence habitat use by coyotes in northwestern Montana. Overlap of habitat use between coyotes and wolves was high; however, partitioning of the use of aspects and areas in proximity to roads may influence the coexistence of these congeneric species.

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