



Large-carnivore response to recreational big-game hunting along the Yellowstone National Park and Absaroka-Beartooth Wilderness boundary

Toni K. Ruth, Douglas W. Smith, Mark A. Haroldson, Polly C. Buotte, Charles C. Schwartz, Howard B. Quigley, Steve Cherry, Kerry M. Murphy, Dan Tyers, and Kevin Frey

Abstract The Greater Yellowstone Ecosystem contains the rare combination of an intact guild of native large carnivores, their prey, and differing land management policies (National Park versus National Forest; no hunting versus hunting). Concurrent field studies on large carnivores allowed us to investigate activities of humans and carnivores on Yellowstone National Park's (YNP) northern boundary. Prior to and during the backcountry big-game hunting season, we monitored movements of grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), and cougars (*Puma concolor*) on the northern boundary of YNP. Daily aerial telemetry locations (September 1999), augmented with weekly telemetry locations (August and October 1999), were obtained for 3 grizzly bears, 7 wolves in 2 groups of 1 pack, and 3 cougars in 1 family group. Grizzly bears were more likely located inside the YNP boundary during the pre-hunt period and north of the boundary once hunting began. The cougar family tended to be found outside YNP during the pre-hunt period and moved inside YNP when hunting began. Wolves did not significantly change their movement patterns during the pre-hunt and hunting periods. Qualitative information on elk (*Cervus elaphus*) indicated they moved into YNP once hunting started, suggesting that cougars followed living prey or responded to hunting activity, grizzly bears focused on dead prey (e.g., gut piles, crippled elk), and wolves may have taken advantage of both. Measures of association (Jacob's Index) were positive within carnivore species but inconclusive among species. Further collaborative research and the use of new technologies such as Global Positioning System (GPS) telemetry collars will advance our ability to understand these species, the carnivore community and its interactions, and human influences on carnivores.

Key words *Canis lupus*, carnivores, *Cervus elaphus*, cougar, elk, grizzly bear, hunting, *Puma concolor*, *Ursus arctos*, wolves, Yellowstone National Park

Address for Toni K. Ruth, Polly C. Buotte, and Howard B. Quigley: Hornocker Wildlife Institute/Wildlife Conservation Society, 2023 Stadium Drive, Suite 1A, Bozeman, MT 59715, USA; present address for Quigley: Beringia South, 3610 W. Broadwater Suite #111, Bozeman, Montana 59715, USA; e-mail for Ruth: truth@wcs.org. Address for Douglas W. Smith and Kerry M. Murphy: Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, Mammoth, WY 89210, USA. Address for Mark A. Haroldson and Charles C. Schwartz: United States Geological Survey, Interagency Grizzly Bear Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA. Address for Steve Cherry: Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717, USA. Address for Dan Tyers: United States Forest Service, Gardiner, MT 59030, USA. Address for Kevin Frey: Montana Department of Fish, Wildlife and Parks, Montana State University, Bozeman, MT 59717, USA.

Recent efforts to restore ecosystems and biodiversity have focused on carnivores because of their keystone effects (Soulé and Terborgh 1999, Gittleman et al. 2001). Widespread reductions in carnivores worldwide have been the norm due to conflicts with humans, and only within the last 2 decades have restoration efforts increased their abundance and distribution (Gittleman 1996, Maehr et al. 2001). Restored carnivores will once again present management and conservation challenges for humans, and information about the human-carnivore interaction will be essential for successful cohabitation. Studies from relatively pristine systems, where human-carnivore conflicts are generally less frequent, can provide baseline data for management in less pristine systems.

The Greater Yellowstone Ecosystem (GYE) contains the rare combination of an intact guild of large carnivores and human activity widely dispersed in remote areas. Grizzly (*Ursus arctos*) and black bears (*U. americanus*), cougars (*Puma concolor*), and coyotes (*Canis latrans*) recovered naturally post-early-twentieth-century carnivore control (Pritchard 1999); wolves (*C. lupus*) were reintroduced in 1995 and 1996 (Bangs and Fritts 1996, Smith et al. 1999). All of these carnivores are currently being studied and were studied prior to wolf reintroduction (Murphy 1998, Clark et al. 1999). Previous efforts have focused on carnivore-prey interactions (Murphy 1998, Ballard and Gipson 2000) or habitat relationships (Knight et al. 1999), but few have examined carnivore-carnivore (Murphy et al. 1998, Kunkel et al. 1999) or carnivore-human interactions (Van Dyke et al. 1986, Janis and Clark 2002).

We combined the efforts of ongoing, independent studies of 3 large carnivores in the GYE: grizzly bears, cougars, and wolves. These 3 carnivores reduce conflict through habitat separation and, when in contact, interact in a dominance pattern as follows: bear > wolf > cougar (Boyd and Neale 1992, Murphy et al. 1998, Kunkel et al. 1999). Most data documenting this pattern come from kill sites. Our aim was to understand interactions beyond kill sites and include the element of human sport hunting.

We designed a spatially and temporally explicit 3-month study to detect and monitor carnivore-carnivore and carnivore-human interactions on Yellowstone National Park's (YNP) northern range (Houston 1982) and the adjacent Absaroka-Beartooth Wilderness (ABW) in Gallatin National Forest, where human harvest of elk (*Cervus ela-*

phus) and other big game occurs each autumn. We designed the study to examine carnivore movements before and during the backcountry hunting season. Our primary objective was to test the hypothesis that grizzly bears, wolves, and cougars exhibit differential use of YNP and the ABW with the onset of the hunting season. We predicted that 1) grizzly bears would shift use north of the park with the onset of hunting due to carcass gut-pile availability and food potentially available at hunter camps, 2) wolves would shift away from hunter camps into the park due to increased human activity north of the park and prey movements into the park, and 3) cougars would not change their pattern of use across the park border due to their ability to seek prey in areas with a greater degree of topographic roughness (Riley et al. 1999) than where humans or wolves may focus their hunting efforts.

Our independent carnivore studies documented that grizzly bears and wolves can displace cougars from their kills (Murphy 1998) and grizzly bears often interact with wolves at kill sites (Ballard et al. 2003); thus, we were also interested in whether there was spatial interaction within and among the carnivore species. A final objective was to determine whether a combination of habitat components would correctly classify carnivore landscape use in the study area and to select habitat variables that might serve in future analyses. We discuss limitations of the current data set and future research needs.

Study area

The territory of the Rose Creek wolf pack and home ranges of 3 grizzly bears and 3 cougars belonging to 1 family unit defined the study area of approximately 2,900 km². This area encompassed a no-hunting area within YNP and a wilderness hunting unit (Montana Hunting District 316) within the ABW of Gallatin National Forest (Figure 1). In general, the area was bounded on the south by the Yellowstone River (2,000 m elevation) and the north by Buffalo Plateau (3,000 m elevation). Vegetation was sagebrush (*Artemisia tridentata*)-steppe grassland to mid-elevation Douglas-fir (*Pseudotsuga menziesii*) to high-elevation spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) forests (Despain 1990). A cougar hunting season occurred outside YNP from 1 December to 15 February 1999. Both

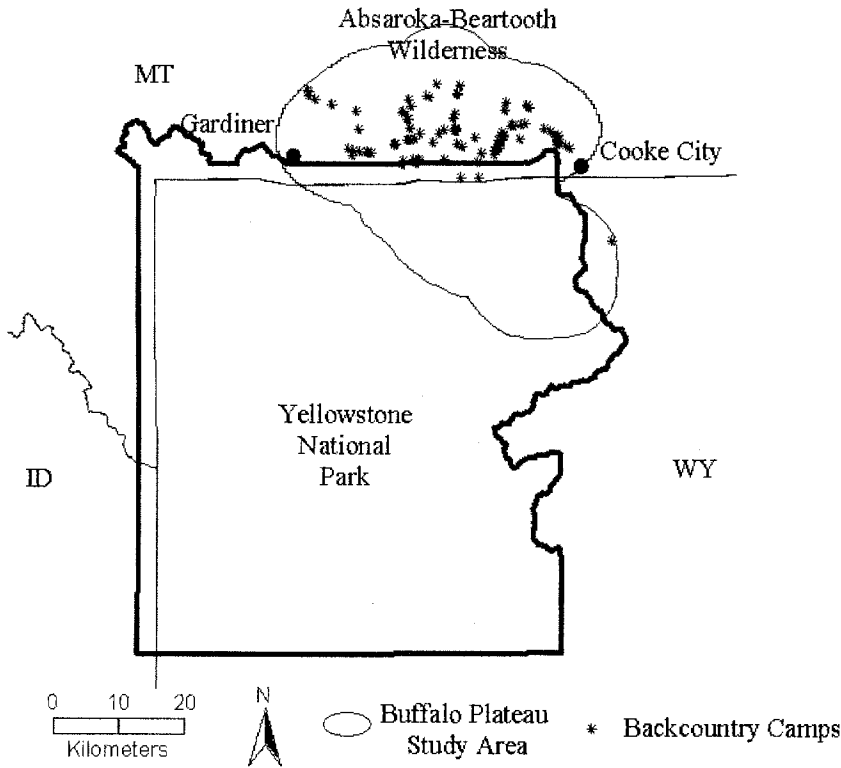


Figure 1. Buffalo Plateau study area where grizzly bear, cougar, and wolf movements were monitored in relation to backcountry hunting camp activity along the Yellowstone National Park and the Absaroka-Beartooth Wilderness boundary, Montana and Wyoming. Two camps shown within the park boundary were established by park rangers to monitor hunting along the park border.

bears and wolves were protected under the Endangered Species Act, which allowed no hunting of wolves (Bangs and Fritts 1996) and permitted take of grizzly bears only in defense of life.

Grizzly bears, cougars, and wolves were sympatric across the study area. Grizzly bears, including all sex-age classes, occurred at an estimated density of 11-17/1,000 km² across the GYE (calculated from: proportion of adult females within population, Eberhardt and Knight 1996; point estimate for reproductive female bears, Keating et al. 2002; current GYE grizzly bear range, Schwartz et al. 2002). The estimated winter density of cougars (minimum number of adults and independent subadults present in 1991) and wolves (adults and pups during the study period) was 21/1,000 km² and 28/1000 km², respectively (Murphy 1998, Smith et al. 1999; Smith et al. 2000). During late summer and early fall, all 3 carnivores overlapped with high-elevation late-summer ungulate range.

Elk, moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) were available as carnivore prey, and backcountry

hunting permits for these ungulate species were issued in fall 1999. Successful hunters discarded approximately 500 tons of meat biomass in the GYE (primarily along the northern and southern boundaries of YNP), with elk parts contributing the largest proportion (74%), followed by mule deer (18%), moose (7.5%), and bighorn sheep (Servheen et al. 1986). Elk were a seasonally (spring and fall) important food source for grizzly bears (Mattson 1997) and an annually important food source for wolves (Mech et al. 2001) and cougars (Murphy 1998). Northern Yellowstone elk numbered approximately 14,538 at the time of the study (minimum count; YNP unpublished data) and were distributed widely both in and out of YNP in the summer, but

migrated to ranges largely within YNP in the winter (Houston 1982, Lemke et al. 1998). The backcountry rifle-hunting season for elk, 15 September-28 November 1999, occurred prior to and during the migratory period.

Methods

Field sampling

We obtained weekly telemetry locations on all radiomarked carnivores that used the study area (3 grizzlies, 3 cougars, and 7 wolves) for 4 weeks (1-31 August 1999) prior to the onset of hunting, daily locations for 14 days (1-14 September 1999) prior to and 16 days (15-30 September 1999) after the onset of hunting, and weekly for 4 additional weeks (1-31 October 1999) during the hunting season. The cougars were a family group consisting of 1 adult female and 2 kittens. The wolves (1 adult male, one 2-year-old, 4 yearlings) were from 1 pack that used a common rendezvous site located just inside the YNP boundary. One wolf (adult female) had dispersed, so we considered movements of this

female independent of other pack wolves. When we saw backcountry hunter camps or kills while searching for focal animals, we recorded their locations. Otherwise, we located backcountry camps via systematic ground surveys conducted by the United States Forest Service and Montana Department of Fish, Wildlife and Parks. We calculated hunter camp-days by summing the number of camps on each day for the duration of the study. We obtained all animal locations from fixed-wing aircraft (Piper Supercub) between the hours of 0655 and 1556. We obtained all locations with a Global Positioning System (GPS) using Universal Transverse Mercator (UTM) coordinates, and we later mapped locations using the Geographic Information System (GIS) software ArcInfo (ESRI, Inc.).

To minimize overflight disturbance to hunters during the hunting season and to estimate telemetry error, we located 8 hidden radiotransmitters from high (2,959 m above mean sea level [MSL]) and low altitude (2,654 m MSL) during the pre-hunt period. After the hunting season began, we located focal animals only from high altitudes and flights were delayed until later in the day to avoid dawn hunting hours. Mean telemetry error was 259 m (95% CI=103–375 m) for high-altitude locations and 184 m (95% CI=120–248 m) for low-altitude locations. We concluded that this error was acceptable to differentiate carnivore locations within or outside YNP.

Analyses

To assess carnivore response to the opening of the hunting season, we pooled grizzly bear locations from 2 individuals with both pre-hunt and hunt data into 1 data set containing 41 locations (Table 1). We pooled grizzly bear locations because

the bears behaved similarly with regard to the onset of the hunting season. One additional bear was killed in a hunting camp on 18 September 1999 after it had previously found food in that camp when it was unattended. This bear was dropped from the hunting-season response analysis because the only hunting-period location was the mortality site. We collapsed cougar locations into 1 data set consisting of 30 locations. Cougar locations were comprised primarily of data from an adult female, but augmented by a yearling offspring's location on days when the mother was not located. Yearling kittens and their mothers travel together and feed at kills during most days, and kitten locations were considered surrogate locations for the adult female. We split wolf data into 2 subsets of 32 and 18 locations. One of the 2 wolf subsets consisted of data from the lone female that had dispersed (Table 1; Wolf 9F). The other wolf subset was comprised primarily of data from an adult male; when he was not located, we used data from other related wolves (Table 1; Wolf 8M). Wolf packs are cohesive and individuals strongly attracted to each other (Mech 1970), so substituting wolf locations for the alpha male with other related members was appropriate. We did not pool the 2 wolf subsets because each behaved differently with regard to preference for area of use. For each species group, we used only 1 location/day in the analysis. On some days there was no location for 1 or more groups, hence the unequal sample size among groups (Table 1).

To test our predictions regarding effect of hunting activity on the 3 carnivores, we bootstrapped confidence intervals about the difference in proportion of locations inside YNP during the pre-hunt minus the proportion of locations outside YNP during the hunt. We derived confidence intervals (95%) for differences in proportions from 10,000 bootstrapped samples. We considered confidence intervals for differences that did not include 0 to be significant.

Table 1. Proportion of telemetry locations for each carnivore subset in Yellowstone National Park (YNP) prior to (pre-hunt) and during (hunt) the elk and big-game hunting season, August through October 1999. Differences in proportions (pre-hunt versus hunt) with 95% confidence intervals (CI) that did not embrace 0 were considered significant. Data subsets were defined by female cougar F47, male wolf 8M, female wolf 9F, and pooled locations of 2 grizzly bears.

Species	Proportion in YNP						
	Pre-hunt	<i>n</i>	Hunt	<i>n</i>	Difference	SE	95% CI ^a
Cougar (F47)	0.40	15	0.87	15	-0.47	0.15	(-0.77, -0.17)
Grizzly (2 pooled)	0.58	19	0.23	22	0.35	0.14	(0.07, 0.64)
Wolf (8M)	0.69	16	0.94	16	-0.25	0.13	(-0.51, 0.004)
Wolf (9F)	0.40	10	0.25	8	0.15	0.21	(-0.27, 0.57)

^a Confidence intervals were derived by bootstrapping proportions 10,000 times.

As a test of interaction within and among species, we estimated the mean and geometric mean distances using paired locations within and among species and

compared them to equivalent values estimated for all possible distances of paired locations within and among species. The resulting Jacobs Index (JI) (Jacobs 1974) returned a value of 0 if the observed and possible distances were the same, increased toward 1 if animals were together, or fell toward negative 1 if animals tended to avoid each other. We used all 180 carnivore locations in this analysis to test for cohesiveness (or avoidance) within a species as predicted (such as attraction between a subgroup of the wolf pack), which would then lend support toward analysis results when testing for attraction or avoidance between different carnivore species. We were unable to test for attraction or repulsion to camps with this index due to the dynamic nature of carnivore movements versus the static nature of hunter camps (Kenward et al. 1993).

We used classification and regression tree (CART) analysis (Breiman et al. 1993) to distinguish habitat use among species and select variables that might be useful in future analyses of carnivore-carnivore interactions. This methodology allowed for a mixture of continuous and categorical variables and did not require any distributional assumption regarding the data. The CART procedure assigned locations to a group based on the values of input variables (Table 2). Successful group assignment, or classification, was dependent on the amount of overlap that existed among groups. If the members

of each group were located in similar habitats, there would not be good separation among groups, and locations may be classified as belonging to the wrong group. Through CART analysis, the variables that contributed the most to separating groups were identified and their relevance can be further explored in future studies.

Due to the exploratory nature of our CART analyses, we imported all 180 carnivore locations into ArcInfo and buffered them using a 375-m radius (the upper bound of the 95% confidence interval for high-altitude telemetry error). In total, we used 11 predictor variables in the CART analysis and included the percent of 1) nonforest, 2) mosaic forest, 3) open forest, 4) closed-canopy forest, 5) cliff, 6) bedrock, 7) no rough, 8) moderate rough, 9) high rough, 10) edge density, and 11) a categorical variable of inside versus outside of YNP.

Type and extent of vegetative cover, edge density, and topographic roughness were estimated for each 375-m-radius area delineated around each carnivore location. We used the vegetation layer developed for the Yellowstone Cumulative Effects Model (R. Maw, database manager, United States Forest Service, Region 4, Ogden, Utah) and collapsed it into 6 vegetation classes (nonforested, mosaic forest, open canopy, closed canopy, cliff, and bedrock) based on hypotheses generated via a priori knowledge of each carnivore in the GYE. The collapsed vegetation coverage was then converted to raster

format with a 30-m cell size, and percentages of each vegetation class were determined. As an index of cover-type heterogeneity, edge density between forested, mosaic, and nonforested cells was calculated as linear m/m² for each location.

We used a 30-m digital elevation model (DEM) to generate an index of topographic roughness using a 90 × 90-m moving window analysis of the absolute value of differences in elevation. The index ranged from 0-100, with 0 being flat and 100 indicating the greatest elevational heterogeneity on

Table 2. Average and standard deviation of predictor variables used in analysis of habitat use among large carnivores in Yellowstone National Park (YNP), prior to and during the big-game hunting season, August through October 1999. A categorical variable, coded as inside or outside of YNP, was included for each location.

Species ^b	Habitat variables ^a									
	Edge density	Not forested	Mosaic	Open canopy	Closed canopy	Cliff	Bedrock	No rough	Moderate rough	High rough
Bears										
Avg	1.1	24.7	28.2	14.7	31.5	0.6	0.3	60.6	33.7	5.7
SD	0.5	23.2	19.8	18.5	25.1	2.5	2.1	24.0	17.7	10.4
Wolves										
Avg	1.2	30.0	24.0	14.3	31.6	0.0	0.1	63.2	31.6	5.2
SD	0.6	27.7	22.7	19.8	27.9	0.1	0.7	30.5	25.1	9.3
Cougars										
Avg	0.5	6.9	11.8	22.5	55.3	3.5	0.1	18.3	51.5	30.2
SD	0.5	13.0	17.6	27.6	31.7	13.6	0.4	19.1	24.8	30.2

^a Edge density was calculated as linear m/m² between forested, mosaic, and nonforested cells in a Geographic Information System. All other habitat variables were calculated as percentages present in 30- × 30-m cells.

^b Descriptive statistics and habitat analyses were based on 180 telemetry locations; 3 grizzly bears with 54 locations, 2 wolf packs with 92 locations, and 1 cougar family with 34 locations.

the study area (e.g., a cliff or very narrow ravine). Based on field-tested break points, this index was collapsed into 3 categories of no, moderate, and high roughness. We used the percent of each roughness category within the 375-m radius as the topographic roughness input variable.

Results

Aerial and ground-based sampling resulted in a total of 92 locations of wolves, 34 locations of cougars, 54 locations of grizzly bears, and 1,063 total hunter camp-days. Of the 180 carnivore locations, 6.7% fell within the telemetry error (± 375 m) of the YNP and ABW boundary. We assumed that telemetry error was unbiased and these locations had equal probability of being either north or south of the boundary with no net influence on our results. Backcountry camps were established from 1 August 1999, prior to hunting, and persisted as late as 31 October 1999. Number of camps observed ranged from 6–12/day prior to the hunting season, peaked at 71/day on the first day of hunting (15 September), and dropped to 1–2/day toward the end of the hunting season (Figure 2).

The 3 carnivores exhibited differential use of YNP versus the ABW with the onset of the hunting season. Grizzly bear response to the onset of hunting was as predicted. The 2 bears were located proportionally more inside the YNP boundary during the pre-hunt period (0.58) than after the hunt started (0.23), indicating that grizzly bears shifted north of the boundary once hunting began (Table 1). Cougar and wolf response to hunting activity differed from our predictions. Proportion of cougar locations inside YNP during the pre-hunt period (0.40) was considerably lower than the proportion

inside YNP after the hunting season began (0.87; Table 1). Both wolf subsets did not change their movement patterns between the pre-hunt and hunting periods. The subset defined by wolf 8M, with their rendezvous site inside YNP, continued high levels of use inside YNP during both the pre-hunt and hunt; conversely, the subset defined by wolf 9F exhibited low levels of use inside YNP during both periods (Table 1).

Measures of association were as expected within species. A female grizzly with cubs showed a neutral association with an adult male ($JI = -0.01$) and a subadult male ($JI = 0.06$). The adult and subadult male bears also exhibited a neutral association ($JI = -0.02$). The cougar individuals showed strong association ($JI = 0.85$), as would be expected for a family group. The wolf data indicated strong association within individuals among the wolf 8M subset of the Rose Creek pack ($JI = 0.34$ – 0.92), and less association between the 2 wolf subsets ($JI = -0.01$ – 0.23). Measures of association among the 3 species were inconclusive. Jacobs Index values ranged from -0.01 – 0.37 for cougar–wolf comparisons, -0.37 – 0.26 for bear–wolf comparisons, and -0.05 – 0.42 for bear–cougar comparisons.

Three of 11 predictor habitat variables separated cougar locations from wolf and bear locations in the CART analysis but were less successful in separating wolf locations (31.5% misclassified as bear) from bear locations (27.8% misclassified as wolf). The amount of topographic roughness and edge density were the most useful variables for separating cougar, wolf, and bear locations. When a location was placed into the CART diagram at the root node, its path in the tree (leading to its classification as cougar, wolf, or bear) was determined by the predictor variables of no topographic roughness

(essentially flat), high topographic roughness, and edge density (Figure 3). For example, a location with less than 29.04% no rough, or flat terrain, in the buffer zone would pass to the left (Figure 3). From that point edge density would be evaluated; if it was less than 0.48%, the location would be classified as a cougar. If edge density was greater than 0.48%, the location would

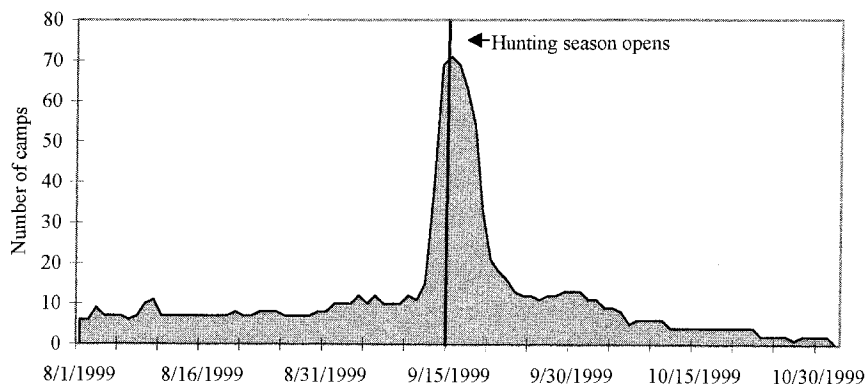


Figure 2. Number of backcountry camps north of the Yellowstone National Park boundary, Montana, 1999. Peak number of camps observed occurred on 15 September.

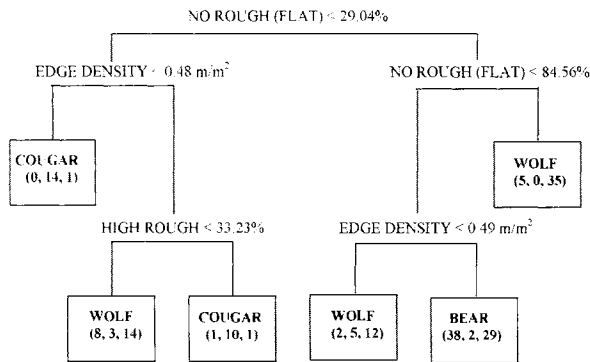


Figure 3. Classification and regression tree (CART) indicating 3 of 11 predictor habitat variables distinguishing among grizzly bear, cougar, and wolf locations. Parentheticals under each carnivore name indicated the number of bear, cougar, and wolf locations that were classified as that particular carnivore species based on each splitting rule. For example, parentheticals in the first box to the right indicated that 5 bear locations, 0 cougar locations, and 35 wolf locations were classified as "wolf" based on the first 2 splitting rules of no rough <29.04% and no rough <84.56%. That is, 35 of 92 wolf locations consisted of primarily flat terrain within the telemetry error buffer around each location.

again be evaluated for topographic roughness in the next step. Locations with little amounts of topographic relief would be classified as wolf, and those with greater amounts would be classified as cougar. We concluded from the CART analysis that during the time we obtained locations, cougars were likely to be located in areas with moderate to high topographic roughness and low edge density (homogeneous forest cover). Grizzly bears appeared to use primarily flat areas with greater heterogeneity for forest cover, and wolves moved through a variety of low and high topographic types and areas with both low and high edge density. In the analysis, 70.6% of cougar locations, 70.4% of bear locations, and 66.3% of wolf locations were correctly classified. Because the predictor variable of pre-hunt versus hunt did not appear in the final classification tree, habitat use did not seem to change based on hunting period for any species.

Discussion

Although we studied a small number of individual animals, and inferences from such data sets are limited, our sample size reflects difficulties associated with studying large carnivores (Gittleman et al. 2001) and the low densities at which their populations occur. The information obtained does suggest that grizzly bears, cougars, and wolves responded differently to the onset of recreational big-game

hunting along the YNP and ABW boundary. The observed shifts of 1) bears toward hunting activity, 2) cougars away from hunting activity, and 3) wolves apparently unresponsive to activity has implications for human-carnivore encounters and the direct mortality to carnivores often resulting from such encounters (Woodroffe 2001, Haroldson et al. 2004).

Our findings for grizzly bears were not unexpected. Bears in the northern and southern GYE exhibited a shift outside YNP during the 1984-2000 hunting seasons (M. A. Haroldson, Interagency Grizzly Bear Team, unpublished data). Timing of shifts in bear distribution associated with hunting supported Haroldson et al.'s (Interagency Grizzly Bear Team, unpublished data) hypothesis that ungulate meat discarded from hunter kills was the primary factor influencing changes in fall distribution of instrumented grizzly bears. August through October coincides with hyperphagia (Nelson et al. 1983) in grizzly bears, and during this period bears are focused on fattening in preparation for winter denning and hibernation. On YNP's northern boundary, bears regularly scavenge gut piles and discarded elk parts as well as check hunter camps for food. Hunters leave an estimated 500 tons of biomass from gut piles and other discarded ungulate remains each year in the GYE, and approximately 370 tons of the biomass is from elk (Servheen et al. 1986). Ungulate remains provide bears with an energetically inexpensive and potentially important food source prior to denning.

The movements of the cougar family, in response to the hunting season, were unexpected because cougars are obligate carnivores and rarely scavenge in northern latitudes (Murphy 1998). Movements of the cougar family may indicate they followed live prey into YNP during the hunt period. Elk avoid areas with high hunter activity (Millsbaugh et al. 2000), and recent data suggested that elk move into YNP when hunting starts (M. Boyce, University of Alberta, personal communication). While cougars prey on mule deer as well as elk, mule deer occur in small numbers and comprise only 3-7% of cougar diet in the study area (Murphy 1998). It is therefore most likely that if the cougar family followed live prey, they were following elk. Cougars may also shift away from increased human activity, and YNP habitats may function as refugia during the hunting season. For example, Florida panthers (*P. c. coryi*) shifted away from trails and onto private land refugia during the hunting season (Janis and

Clark 2002). Belden and Hagedorn (1993) documented that cougars translocated into northern Florida abandoned their newly established home ranges after the onset of the deer-hunting season. However, our data set was limited to daytime locations on 1 cougar family, and other factors besides hunter activity and elk distribution may influence cougar movements during the hunting season.

Like cougars, the wolf response to hunting also was not predicted. Yellowstone wolves are generally more visible than cougars or bears, possibly making them more apt to respond to human hunting activity via direct contact. This factor contributed to our prediction that wolves would shift away from increased human activity. The lack of detectable response to hunter activity may be due to behavioral plasticity of wolves to humans, which has been recorded elsewhere (Mech 1995), or it suggested an opportunistic foraging strategy of wolves for live prey and hunter-created carrion. These factors likely contributed to the lack of observed effect, but will require further study to understand more completely.

Other factors that could affect the observed results were distribution and abundance of other autumn food sources for the bears or interactions between the 3 species. Grizzly bears may shift north of the YNP boundary during the hunting season to access whitebark pine cones, which mature during early fall and provide an important food source for bears (Blanchard 1990, Mattson 1997). However, timing of shifts in grizzly bear distribution in the GYE were correlated with the opening of hunting seasons, occurred during both good and bad seed crop years, and were not attributed to bears searching for seeds of whitebark pine (M. A. Haroldson, Interagency Grizzly Bear Team, unpublished data).

Interspecific interactions mediated by the presence of carrion or shifts by prey may also

play a role in carnivore movements. In particular, increased seasonal bear densities during a time when searches for carrion are intensified may affect subordinate competitors such as cougars. The observed shifts by the cougar family group may have been in response to interactions with bears and wolves that encounter and kleptoparasitize cougar-killed prey (Murphy et al. 1998, Kunkel et al. 1999). Grizzly bears may also respond to wolf kills and interact with wolves at kill sites (Figure 4; Ballard et al. 2003). Direct interactions at kill sites can be fatal to 1 or both species involved (Boyd and Neale 1992). In addition, spatial-temporal shifts associated with carrion availability or prey movements may bring carnivores into direct conflict with conspecifics, increasing the risk of intraspecific aggression and mortality (Janis and Clark 2002). Our limited data set and analyses failed to reveal any direct interactions between the 3 species, and we believe observed shifts were likely due to the hunting season. However, a larger sample of radiomarked animals and sampling across diurnal and nocturnal hours is necessary to fully understand patterns of interaction within and between species.

The role that habitat characteristics play in carnivore movements during increased human activity, or avoidance of interspecific competitors,



Figure 4. Grizzly bears tended to be dominant at carcasses killed by cougars, wolves, or humans and actively searched for carrion during hyperphagia, which coincided with the early-season elk hunt along the Yellowstone National Park and Absaroka–Beartooth Wilderness boundary. Photo by Douglas W. Smith, July 2000.

is poorly understood. Our time-limited location data indicated that during diurnal hours, grizzly bears were located in areas with high edge density and low topographic roughness. Bear preference for high-elevation open-timber edges in YNP has been documented (Blanchard 1983). In direct contrast, steep mountain slopes or abundant horizontal and vertical cover provided by vegetation and topography are important habitat components for cougars (Williams et al. 1995). Our data indicated that when the cougars used sites with less edge density, they were more likely to be in areas with high topographic roughness, which provided security from competitors and disturbance, especially important for females with dependent young. Wolves may be more flexible in their use of habitat, moving through a variety of forest cover types and terrain features. Understanding how the large carnivore guild uses habitat components in the presence and absence of each other, as well as during increased human activity, should be investigated further. We are continuing to coordinate our species-focused projects to accomplish this.

Increased human presence in early-season hunting units increases potential for conflicts between large carnivores and humans and is a major cause of carnivore mortality, even in protected areas (Woodroffe 2001). Numbers of hunting-related grizzly bear mortalities increased in the GYE during the 1990s, and nearly half this increase was due to bear deaths occurring in early hunt units during September (Figure 5; M. A. Haroldson, Interagency Grizzly Bear Team, unpublished data). The seasonally high density of bears and increased hunting-related mortalities may be exacerbated by an increasing (Eberhardt 1995, Boyce et al. 2001) and expanding (Schwartz et al. 2002) grizzly bear population. A considerable portion of cougar-human conflicts in western Montana occur during the general deer and elk hunt (September through November), particularly in areas where roads and snow machines allow greater access for hunters (K. Aune, Montana Department of Fish, Wildlife and Parks, personal communication). While other studies also do not record a wolf response to the onset of ungulate hunting season, human-caused wolf mortality typically increases at this time (Fuller 1989). Besides direct mortality that may occur to carnivores, another issue is that human safety may be compromised by interactions with carnivores attracted to discarded elk parts and hunter camps.



Figure 5. Grizzly bears checked hunter camps for anthropogenic foods and regularly scavenged hunter-discarded ungulate remains. While ungulate remains provided bears with a potentially important food source prior to denning, attraction to these food sources may compromise human safety and survival of individual bears. Photo by Mark Brusino, October 1995.

Further study of carnivore and prey movement response after hunting abates is necessary to elucidate length of disturbance response. During most years, the majority of hunter harvest of elk occurs during the first week of the hunting season (K. Frey, Montana Department of Fish, Wildlife and Parks, personal communication), and presence of hunter camps quickly declined to pre-hunt levels (≤ 10 camps/day) within the first 7-10 days during our study. Understanding whether carnivore or prey response to hunting is of short or long duration will influence possible adaptive management schemes, particularly for species most impacted via direct mortality (i.e., grizzly bears) or in more highly fragmented systems where shifts in carnivore and prey movements bring them into further conflict with humans.

Conclusions and future direction

Management of large carnivores will continue to challenge wildlife managers. The future existence of carnivores depends on how well we understand anthropogenic effects and manage carnivore-human interactions. Our study suggested that the onset of elk hunting north of YNP did affect carnivore distribution. Although we did not record a wolf response, results indicated that where humans and carnivores overlap during the hunting season, management attention is warranted. Further information needs to be gathered on carnivore-carnivore interactions and cougar and wolf response to recreational hunting.

Protecting large, intact areas that serve as refuge habitat where carnivores and prey can meet their ecological requirements and minimize impacts from human activity will be important for long-term carnivore conservation. Recent studies have shown that combined effects of roads, hunters, and conflicts with humans along reserve boundaries have contributed significantly to the extinctions of large carnivores, particularly in small reserves (Sunquist and Sunquist 2001, Woodroffe 2001). For example, Eurasian badgers (*Meles meles*) and Iberian lynx (*Lynx pardinus*) incurred high mortality at the border of Doñana National Park, Spain, due to human poaching of ungulates along the border (Revilla et al. 2001). Carnivore-carnivore competition and carnivore-prey interactions may further influence these negative effects, and knowledge of ecological relationships between carnivores will have implications for conservation efforts (Creel et al. 2001). In addition, reserves, multi-use lands, and landscape linkages should be managed and conserved to provide the diverse habitats cougars, bears, and wolves need for hunting prey, escape cover from humans and other carnivores, and seasonally ephemeral foods for bears.

In the GYE, recent studies indicated that rural residential development is increasing rapidly because of natural amenities associated with the area (Hansen et al. 2002). People attracted to lands surrounding reserves may impact the natural buffers of those reserves and alter the ecosystems and ecological process within them (e.g., exotic weeds, wildlife diseases, fire suppression; Hansen et al. 2002). As human development and recreational use increase, managers of large carnivores within and adjacent to the GYE need new paradigms (Hansen et al. 2002) in land management that consider multispecies behavior and ecosystem processes along with the differing objectives of management jurisdictions.

Our collaboration, data, and results provide a springboard to expand our multi-species research efforts. Our data set was limited in providing an understanding of the role recreational hunting played in influencing carnivore response to human activity. Because recreational elk and big-game hunting occurs in wilderness settings adjacent to park lands in the GYE, an opportunity exists to re-examine cougar, wolf, and grizzly bear response to recreational hunting. Repeating our study with the use of GPS-marked carnivores and focusing more closely on prey and hunter movements in a north-

ern and southern study area may elucidate factors affecting carnivore response to hunting. It is timely to advance our knowledge of these species. Worldwide, examples exist of vanishing carnivores and the urgent recovery efforts for these species and their habitats, most of which are hampered by a lack of time and information. These are monetarily and ecologically costly activities, making it imperative that we gain reliable knowledge about large-carnivore guilds and their interactions to make our efforts more efficient and effective.

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Toni K. Ruth (second from right) is an associate conservation scientist with the Wildlife Conservation Society and project leader researching the effects of wolf reestablishment on the cougar population in Yellowstone National Park. She received

her B.S. in forest and resource conservation from the University of Florida, an M.S. in wildlife science from Texas A&M University, and is a Ph.D. candidate in wildlife ecology at the University of Idaho. She previously worked with the Hornocker Wildlife Institute for 10 years and has been involved in cougar research in various ecosystems since 1987. Her interests include ecological relationships and interactions between carnivores, prey, and humans, particularly research in multi-carnivore/multi-prey systems. **Douglas W. Smith** (second from left) is project leader for the Yellowstone Gray Wolf Restoration Project in Yellowstone National Park and has been with the program since its inception. Doug has studied wolves for 23 years. He received his B.S. in wildlife biology from the University of Idaho, M.S. in biology from Michigan Technological University, and Ph.D. from the University of Nevada, Reno in ecology, evolution, and conservation biology. Doug has produced numerous publications on both the wolf and the beaver and co-authored the book, *The Wolves of Yellowstone*. **Mark Haroldson** (left) is a supervisory wildlife biologist for the USGS Interagency Grizzly Bear Study Team. Mark received his B.S. in wildlife biology from the University of Montana in 1979, and has studied grizzly bears in the Yellowstone Ecosystem since 1984. **Polly Buotte** (third from left) is a field biologist with the Wildlife Conservation Society. She received her B.S. in wildlife biology from Colorado State University and her M.S. in wildlife biology from the University of Montana. She has been with the Hornocker Wildlife Institute/Wildlife Conservation Society's Yellowstone Cougar Project since January 2000. **Chuck Schwartz** (front center) is currently leader of the Interagency Grizzly Bear Study Team for the Greater Yellowstone Ecosystem. He received his Ph.D. from Colorado State University. His research interests are carnivore ecology and management, predator-prey dynamics, and conservation of bears. Chuck has been a member of The Wildlife Society since 1968. **Howard Quigley** (back right) is a senior ecologist with Beringia South, a nonprofit science and education group in Kelly, Wyoming. He received his B.S. from the University of California at Berkeley, M.S. from the University of Tennessee at Knoxville, and Ph.D. from the University of Idaho at Moscow. He has worked on a variety of large carnivores around the world and continues to coordinate multi-carnivore research and conservation efforts in the Greater Yellowstone Ecosystem. **Steve Cherry** (back left) is an associate professor of statistics at Montana State University. He has a B.S. in applied mathematics from North Carolina State University, an M.S. in ecology from the University of Tennessee, and M.S. and Ph.D. degrees in statistics from Montana State University. He is primarily interested in applications of statistics in the environmental and ecological sciences and is a member of the Interagency Grizzly Bear Study Team. **Kerry Murphy** is a wildlife biologist employed by the U.S. National Park Service, Yellowstone National Park. He received his Ph.D. in forestry, range, and wildlife science from the University of Idaho in 1998 and his M.S. in wildlife biology from the University of Montana in 1983. His professional interests include the ecology and management of carnivores and endangered species. **Dan Tyers** is a district wildlife biologist with the United States Forest Service on the Gardiner Ranger District, Gallatin National Forest. He has a Ph.D. in wildlife biology from Montana State University. **Kevin Frey** has been a grizzly bear management specialist with Montana Fish, Wildlife and Parks since 1993, and oversees the north and west portions of the Yellowstone Ecosystem. He received a B.S. in fish and wildlife management from Montana State University in 1982. Kevin has worked on various black bear and grizzly bear research projects in Montana, Idaho, and Wyoming since 1976.

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