EFFECTS OF WOLF REINTRODUCTION ON A COUGAR POPULATION IN THE CENTRAL IDAHO WILDERNESS

JAMES AKENSON, University of Idaho, Taylor Ranch Field Station, Cascade, ID 83611, USA
Email: tayranch@direcpc.com
HOLLY AKENSON, University of Idaho, Taylor Ranch Field Station, Cascade, ID 83611, USA
Email: tayranch@direcpc.com
HOWARD QUIGLEY*, Hornocker Wildlife Institute, 2023 Stadium Drive, Suite 1A, Bozeman, MT 59715, USA *present address: P.O. Box 147, Kelly, WY 83011

Abstract: Wolves (*Canis lupus*) were reintroduced in the central Idaho wilderness in 1995 and 1996 and rapidly established packs in areas previously occupied by cougars (*Puma concolor*). We spent four winters studying the relationship between sympatric wolves and cougars in the Idaho wilderness, beginning work the first year the two carnivores coexisted. We examined the potential for competition during winter between resident cougars and a newly established wolf pack for food, space, and habitats through radio telemetry tracking and examination of 192 carcasses. We found that wolf and cougar diets were almost identical. Winter home ranges of wolves and cougars overlapped, although the wolf pack home range size was 2-20 times the size of individual cougar home ranges. We observed wolf utilization of cougar-killed prey and evidence of wolf avoidance by cougars. Although no interspecific killing was documented between wolves and cougars, the effects of competition, a declining prey population, and heavy hunter harvest of cougars were expressed by low recruitment, decreased adults, and disrupted social structure in the cougar population. A large-scale wildfire provided a unique opportunity to compare wolf and cougar responses to catastrophic environmental change. Wolves, with large home ranges, were more adaptable to change than were cougars. For cougars, the combination of decreased prey numbers, low reproductive rate, high hunter harvest, and large-scale habitat alteration from fire appeared to amplify the effects of competition from the recently established wolf pack and increased intraspecific strife. The cougar population experienced a period of instability during this study, as cougars adapted to coexistence with another large carnivore in a dynamically changing environment.

Proceedings of the Eighth Mountain Lion Workshop

Key Words: *Puma concolor*, competition, cougar, wolf, *Canis lupus*, Idaho, predation, carnivore, ungulates, fire.

INTRODUCTION

Prior to 1900, wolves and cougars coexisted in central Idaho, but by the turn of the century settlers had moved into the Big Creek drainage in the rugged Salmon River Mountains to mine for gold, trap, and establish homesteads. Hunting, trapping, and poisoning of carnivores were common practices, and by 1895 sightings or evidence of wolves in the drainage were uncommon (Caswell 1895). Despite the remoteness of the area, ungulate and carnivore numbers varied dramatically over the next 100 years, often in response to human hunting, trapping, and poisoning efforts (Figure 1). The ecology and population dynamics of cougars in the Big Creek drainage have been well documented and described over the past 40 year, starting with

Hornocker's benchmark cougar population and ecology research from the 1960's (Hornocker 1970). Seidensticker et al. (1973) then elucidated the social organization of cougars and contributed additional information on this cougar population and its food habits. Koehler and Hornocker (1991) compared resource use among cougars, bobcats, and coyotes. Quigley et al. (1989) found that cougar numbers in the Big Creek drainage had increased over a 20-year period in correlation with an increase in elk numbers since the 1960s. In 1995 and 1996 the U. S. Fish & Wildlife Service reintroduced 35 wolves into the central Idaho wilderness, as part of the restoration of wolves to the northern Rocky Mountains. Two of these wolves became the breeding pair of the Chamberlain Pack in 1996 and established a home range that included the Big Creek drainage.

There is strong potential for competition between the recently introduced wolves and resident cougars, because both large carnivores primarily prey on large ungulates and have similar diets when they occur together (Husseman et al. 2003, Kunkel et al. 1999, Ruth 2004b). Competition could be expressed through one species killing the other: as Boyd and Neal (1992) and Ruth (2004b) found with adult cougar mortality in Glacier National Park and Ruth (2004a) documented with cougar kitten mortality in Yellowstone National Park, or cougars could kill wolves. Exploitation competition can occur when these sympatric species share the same food, space, or habitat resources. Interference competition can occur when one species interacts with the other, such as wolf displacement of cougars from their kills. Competition can result in decreased reproductive success or survival of one or both species or lead to resource partitioning to decrease competition (Colwell and Futuyma 1971). Kunkel et al. (1999) found evidence of exploitation and interference competition following wolf recolonization of cougar habitat in northwest Montana, but stated that wolves and cougars had not yet partitioned food resources or space. In assessing the magnitude of the effect of wolf reintroduction on ungulate populations, it is necessary to understand whether wolf predation will be additive to other causes of mortality or be partially offset by changes in predation by other large carnivores such as cougars. Kunkel and Pletscher (2001) determined cougar and wolf predation on white tailed deer (*Odocoileus virginianus*) in Montana was primarily additive. Cougar numbers and distribution could decline as a result of wolf competition, affecting sport hunting harvest of ungulates as well as cougars. A simultaneous investigation of wolves and cougars provides valuable insights into the influence they have on each other and their combined effect on prey species. Results from this study will guide resource managers in understanding the integrated impact of these sympatric large carnivores on ungulate prey. Furthermore, information from this research is essential for predicting the outcome of wolf recolonization or reintroduction in other areas where cougars occur. The objectives of our study were 1) to assess wolf-cougar-prey dynamics in a wilderness setting, 2) assess competition and resource partitioning of food, space, and habitat between cougars and wolves, and 3) document interspecific interactions and killing between cougars and wolves.

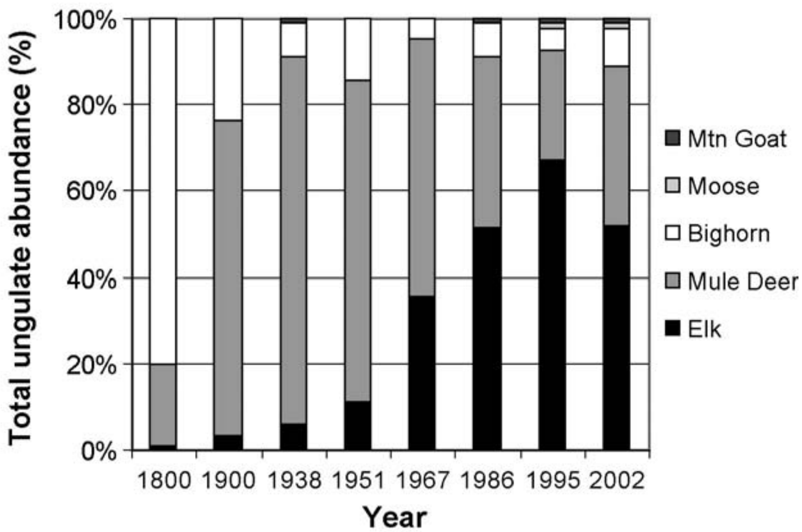

Figure 1. Relative ungulate abundance on Big Creek, from 1800 to 2002. (Unpublished data assimilated from Caswell 1895: Payette National Forest, McCall, Idaho, USA, Idaho Department of Fish and Game, McCall, Idaho, USA)

STUDY AREA

Research was conducted from University of Idaho's Taylor Ranch Field Station on Big Creek, in the Frank Church - River of No Return Wilderness (FC-RNRW) in Idaho (Figure 2). The Big Creek study area is in the center of the 9,550 km^2 FC-RNRW, and surrounded by an additional 6,450 km^2 of designated wilderness. The 550 km^2 study area is the Big Creek winter range for elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*). Terrain is steep and dissected by the east flowing Big Creek drainage and its tributaries. Bunchgrass slopes, mountain mahogany (*Cercocarpus ledifolius*) outcrops, and open Douglas fir (*Pseudotsuga menziesii*) forests dominate south aspects; dense Douglas fir forests occur on north aspects, with deciduous vegetation (*Populus trichocarpa*, *Alnus incana*, *Betula occidentalis*) in narrow riparian zones. The winter range is semi-arid; annual precipitation at Taylor Ranch Field Station is 38 cm. Elevations range from 1,200 to 2,200 meters. Native ungulates are migratory and include elk, mule deer, bighorn sheep, moose (*Alces alces*), and mountain goats (*Oreamnos americana*). Over the past century, the Big Creek large carnivore community has consisted primarily of cougars, black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*), while wolverine (*Gulo gulo*), fisher (*Martes pennanti*), lynx (*Lynx canadensis*), and the occasional grizzly bear (*Ursus arctos*) have also been present. During the same time period, state and federal agency records and historical documents indicated that the numbers and relative abundance of the ungulate species have varied considerably (Figure 1). Bighorn sheep and mule deer were the most common ungulates on Big Creek 100 years ago (Caswell 1895), but elk colonized the area in the 1940s (Coski, Trueblood, and Manis. 1940. USFS unpublished winter range ungulate surveys of Big Creek, 1940, Payette National Forest, McCall, Idaho, USA) and increased in numbers until they peaked in the mid 1990s (Idaho Department of Fish and Game unpublished data, McCall, Idaho, USA). Elk productivity decline to 17 calves per 100 cows in 1995, a few years before the Chamberlain Wolf Pack established a winter home range on Big Creek, reached a low of 7 calves per 100 cows in 1999 and increased to 21 calves per 100 cows in 2003. Since 1986, elk numbers have exceeded mule deer numbers. Elk, mule deer, bighorn sheep, moose, cougars, black bears, and bobcats are hunted species. Mean population estimates for ungulates during 1999-2002 were 1185 elk, 650 mule deer, 150 bighorn sheep, and 30 moose.

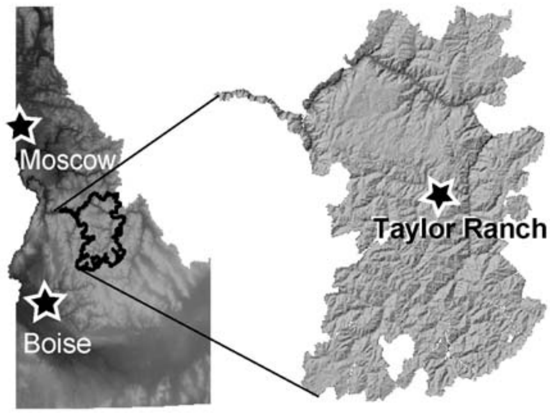

Figure 2. Frank Church River of No Return Wilderness in Idaho and location of Taylor Ranch Field Station on Big Creek.

METHODS

Our study began in the 1998-1999 winter and we monitored wolves and cougars four winters, December through April. The Chamberlain Pack breeding pair were both radio collared in Canada prior to their release in Idaho in 1995. They had their first litter of pups in 1996 and by 1998 there were 7 individuals in the pack. We captured and radio collared 8 cougars from 1999 to 2001 using trailing hounds. Cougars were immobilized with ketamine and xylazine in accordance with the Hornocker protocol (Quigley 2000). Cougar capture and handling was authorized through University of Idaho Animal Care and Use Committee Protocol 1999-23.

We evaluated carnivore competition by comparing food habits. To do this, we intensively searched for kill sites along trail systems, ridgelines, and canyon bottoms within the study area. We travelled up to 30 km daily searching for kill evidence including localized scavenger bird activity, tracking and back-tracking wolf and cougar tracks, and looking for carcasses and blood in the snow. All of our field logistics involved ground travel, either on foot, using snowshoes, or by riding mules, and was supported by aerial telemetry. Once a carcass was located we examined the carcass and surrounding area to determine cause of death and which carnivore made the kill if mortality was due to predation. We collected and dried marrow fat from femurs and calculated percent femur fat using techniques by Neiland (1970). We had an incisor tooth sample from each carcass aged through cementum annuli analysis (Matson's Laboratory, Milltown, MT, USA). We categorized our confidence in identifying the predator as *possible*, *probable*, or *positive*. The latter two categories, indicating higher certainty, were used for comparison following the protocol of Murphy (1998). We also used snow tracking or remote cameras to document scavenging activities.

Winter seasonal home ranges of a Chamberlain Wolf Pack member and 5 cougars were calculated from 95% and 50% fixed kernel home range analyses using the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView Geographic Information System (GIS, Environmental Systems Research Institute, Redlands, California, USA). A minimum of 30 locations per seasonal home range estimate were obtained through weekly aerial telemetry flights and ground locations at least 2 days apart. We used chi-square analysis to test for differences in sympatric cougar and wolf diets. Chi-square analysis was also used to compare the proportion of calf elk killed by cougars and wolves and the proportion which occurred on the study area, as well as to compare age distributions. Differences in the two carnivores' intensity of scavenging and preying on animals in poor condition were also evaluated using chi-square analysis.

RESULTS

Reproduction and Mortality

Reproductive success was monitored for both species. The Chamberlain wolf pack size in winter was typically seven to ten wolves. The mean litter size for wolves was 4.8 pups per year. By contrast, the cougar population changed from ten to six resident adults during the study period. Four to six adult cougars were females, producing a total of 1.5 litters per year. Mean litter size was slightly under two kittens per litter. Mortality was monitored over the four-year period with two of five collared wolves dying from illegal human caused mortality. Six of seven radio instrumented cougars died during the study. A total of 20 cougar mortalities were documented in this four-year period, including 14 from hunting, 3 from intraspecific strife, 1 starvation, 1 foot injury/starvation, and 1 killed by wildfire. Hunter harvest represented 44% annual removal of the adult resident cougar population.

Home ranges

The Chamberlain Wolf Pack's winter home range, 1,130 km^2 (95% fixed kernel), was significantly larger than individual cougar winter home ranges and encompassed two ungulate winter ranges. The wolf pack was very mobile, spending time in both the Big Creek and Chamberlain Creek ungulate winter ranges (Figure 3 and 4). In contrast, 3 female cougar winter home ranges were 40.9 km^2, 57.4 km^2, 261 km^2, and two male cougar winter home ranges were 618 km^2 and 398 km^2 (95% fixed kernel). Aerial telemetry locations revealed a high degree of winter home range overlap between radio-collared cougars and the Chamberlain wolf pack, with the wolf home range encircling 4 of 5 cougar home ranges in 2000 (Figure 3). The proportion of time the wolf pack spent on the Big Creek winter range varied from 27% prior to the study period to 78% during the study (Figure 4). A large-scale wildfire (700 km^2) burned over 80% of the study area in August of 2000. The fire caused extreme habitat alteration, initially a loss of ungulate winter forage in 2001, then an abundance of nutrient rich grasses, forbs, and shrubs in the following years. In response to the lack of food on the burned winter range, many Big Creek elk migrated to the Chamberlain Creek winter range in the winter following the fire, but returned to the Big Creek the next winter. The wolf pack also avoided Big Creek in 2001; instead it switched its primary use to the Chamberlain winter range (Figure 4). Cougars remained in their Big Creek home ranges in winter 2001 despite the burn and preyed more on alternative food resources such as moose, beaver, coyote, and eagle since fewer elk were available (Figure 5). As a result of the wildfire, there are two winters of pre-fire and two of post-fire data.

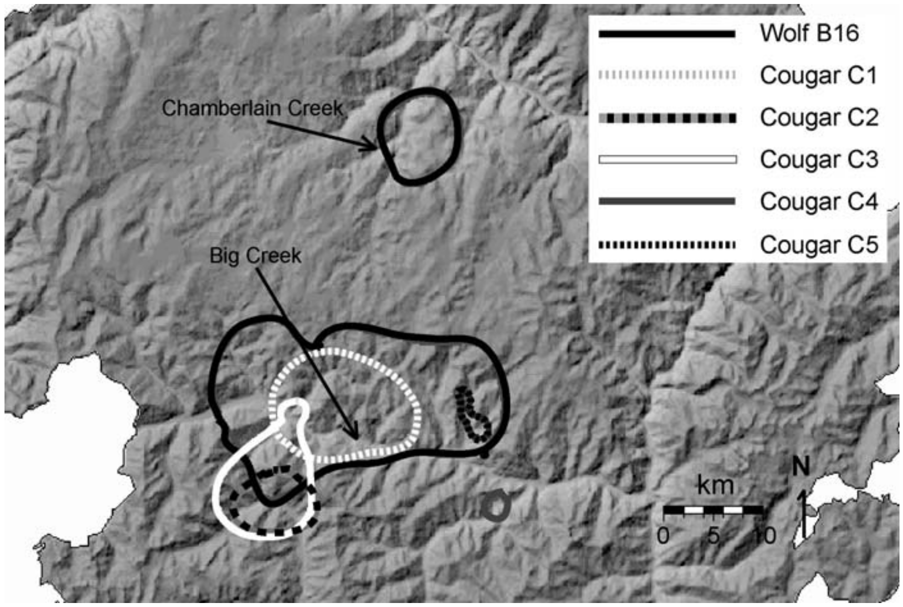

Figure 3. Chamberlain alpha male wolf B16 and 5 cougar winter home ranges (50% fixed kernel home ranges) in the FCRNR Wilderness.

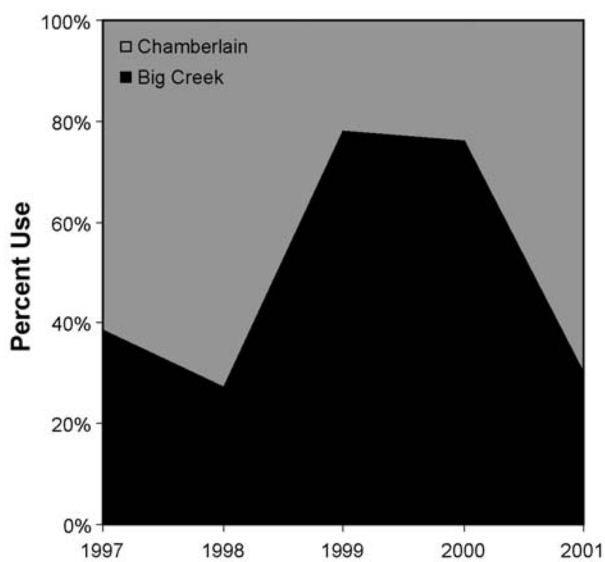

Figure 4. Chamberlain Wolf Pack use of two ungulate winter ranges: Chamberlain Creek and Big Creek.

Food Habits

We investigated 192 carcasses during the four winters. Among these carcasses, 84 were cougar kills and 51 were wolf kills. Both cougars and wolves preyed predominantly on elk and mule deer, although cougars had a more diversified diet, particularly after the 2000 fire (Figure 5). In areas where both wolves and cougars occurred, their proportional utilization of elk and deer was the same (χ^2 p = 0.747; Figure 6). In these areas where home ranges overlapped, neither cougars nor wolves exhibited prey selection between elk and deer; instead, both carnivores killed the two ungulates in the same proportions as the relative abundance of elk and deer within the Big Creek winter range area of overlap (cougar χ^2 p = 0.645, wolf χ^2 p = 0.997; Figure 6). Wolves killed a higher proportion of calf elk (48%) than did cougars (24%; χ^2 p = 0.048) and both species selected for calves when compared to the proportion of calves in the elk population (11%; cougar χ^2 p = 0.011, wolf χ^2 p = 0.001). The Big Creek elk population had a high proportion of older aged cows, as suggested by the 9 year old median age of hunter harvested cow elk during the study period. Cougars and wolves killed many older aged cow elk (cougar median elk age 13, wolf median elk age 11). There was no significant difference in the age distribution of elk killed by cougars and wolves (χ^2 = 2.91, p = 0.406; Table 1) and neither carnivore killed elk with a different age class distribution than hunters (cougar χ^2 = 3.13, p = 0.372; wolf χ^2 = 7.30, p = 0.063; Table 1). We found no difference in the proportion of kills that had severely depleted femur fat between wolf-killed elk (36%) and cougar-killed elk (20%; χ^2 p = 0.194).

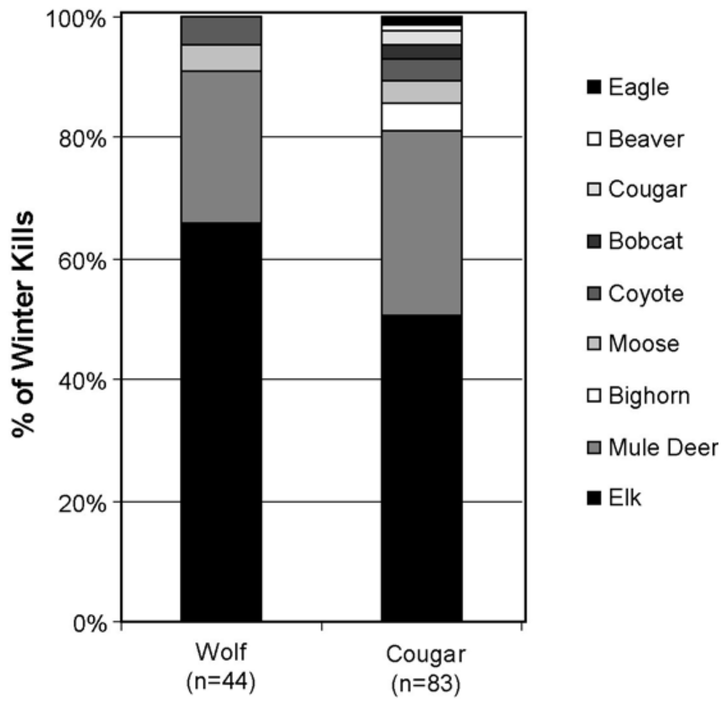

Figure 5. Winter food habits of wolves and cougars in the Big Creek study area, 1999-2002.

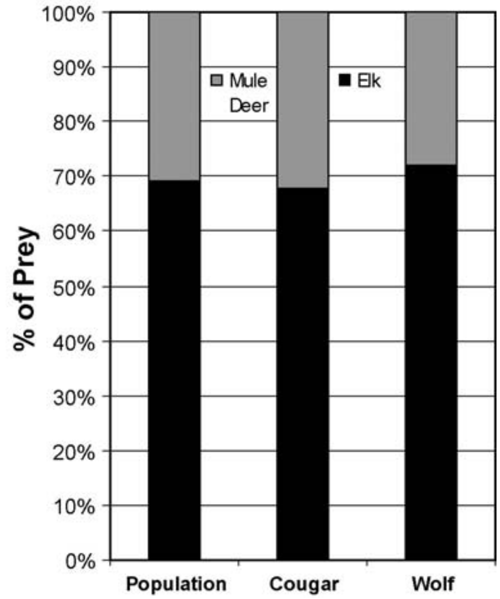

Figure 6. The proportion of elk versus deer killed by sympatric wolves and cougars during winters 1999-2002 and a comparison to the relative abundance of the two ungulates in the Big Creek area of home range overlap.

Table 1. Age distribution of female elk and calves killed by cougars, wolves, and hunters.

Elk Age	Cougar kills	Wolf kills	Hunter harvest
Calf	10	11	2
Yearling	3	0	0
2-8 yrs	8	4	9
9-20 yrs	21	8	14

Interactions

We did not document any fatal interspecific interactions between wolves and cougars; however, we did document three cases of mature male cougars killing other male cougars, one occurrence of a female cougar with kittens feeding on one of the dead male cougars, and one incidence of wolves feeding on one of the dead male cougars. Wolves visited or scavenged cougar kills much more often (18%) than cougars visited wolf kills (4%; χ^2 p = 0.019, n = 84 cougar kills and 51 wolf kills). The proportions of carcasses scavenged by wolves and cougars were nearly identical to the findings of Ruth (2004b) in Glacier National Park. We found evidence that two cougars were treed by wolves at cougar kills (mule deer and bighorn sheep); the cougars abandoned the carcasses and wolves usurped the kills. We documented long distance movements by 2 cougars up to 2 days after wolves arrived in their home range, but were unable to statistically evaluate these movements. The cougar often moved to a distant edge of its home range when wolves were present in its home range, suggesting avoidance behavior (Figure 7).

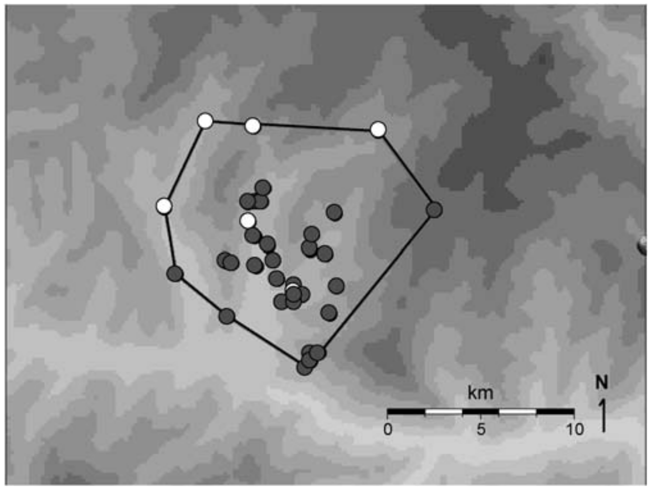

Figure 7. Cougar avoidance of wolves: Female cougar C-5's year 2000 winter home range (100% MCP) and locations. The 6 white circles were cougar locations immediately following the 6 occasions when wolves arrived in the cougar's home range; grey circle cougar locations were when wolves were not in the cougar's winter home range.

DISCUSSION

Potential for Competition

We found potential for interspecific competition between the resident cougar population and a reintroduced wolf pack on the Big Creek study area, including home range overlap and shared food resources. The 2 large carnivores shared much of the Big Creek ungulate winter range; the wolf pack home range encompassed most of the cougar home ranges on Big Creek except for those in steeper, rockier, and more arid section of the drainage. Sympatric cougars and wolves on Big Creek had similar food habits and shared the same prey populations, thus competing for the same food resources. While Kunkel et al. (1999) found cougars and wolves both selected white-tailed deer over elk, Husseman et al. (2003) found wolves selected elk over deer, and Hornocker (1970) documented that Big Creek cougars selected elk over deer; we did not find any diet selection by wolves or cougars. Like Husseman et al. (2003) we found besides having similar diets, wolves and cougars both selected calf elk over adult elk. The combined predation of cougars and wolves on ungulates could result in decreased prey numbers, further increasing competition. In fact, the Big Creek elk population did decline 20 percent during the study period, and it had declined 15 percent in the 4 years prior to research. The declining elk population, as well as large-scale wildfire, have exacerbated interspecific competition.

Many environmental and temporal factors play into interspecific competition. Koehler and Hornocker (1991) researched competition between mountain lions, bobcats and coyotes in this same study area from 1980-1985. They observed that during winter interspecific competition increased due to both predators and prey congregating at lower elevations. This increased density of food resources resulted in more frequent predator contact. Cougars proved to be the dominant competitor in this drainage 20 years ago, with both bobcats and coyotes incurring fatal consequences, particularly when visiting cougar kill sites.

Expression of Competition

Direct interspecific mortality was not observed between cougars and wolves on Big Creek, however, cougar behavior including treeing from wolves, moving from kills and avoiding wolf contact, and a low incidence of kittens suggested cougars experienced or perceived a threat from encounters with wolves. Interspecific competition can result in decreased reproductive success and increased mortality, leading to population declines. Reproduction and recruitment of subadult cougars on Big Creek was half that documented by Hornocker (1970) from the same study area in the 1960s. For 5 years, we monitored a newly independent resident female cougar that interacted with wolves. During that period, we did not find evidence that she had kittens with her, although we did document her (consorting) with male cougars on several occasions. In both study years post forest fire this cougar exhibited natal localization behavior described by Seidensticker (1973). However, follow-up monitoring did not verify that she had kittens at heel. Murphy (1998) defined female cougar reproductive success as the ability to raise a litter of kittens to dispersal age. Both Murphy (1998) and Logan (2001) noted that reproductive success of female cougars is highly variable and Robinette et al. (1961) found that one sixth of mature female cougars he sampled had never been pregnant, so we do not dare draw conclusions based on the reproductive success of only one female. However, during the same years post forest fire, we only documented one other female cougar track with a single kitten.

Cougar mortality during 1999-2001 was much greater than that reported for the same study area in 1960s (Hornocker 1970), 1970s (Seidensticker et al. 1973), and 1980s (Quigley et al. 1989), primarily due to high hunter harvest, but also due to intraspecific strife and starvation. High cougar harvest during the study period probably decreased interspecific competition, but wolf competition, coupled with low reproduction and apparent year-long vacancies in 2 female home ranges may slow or inhibit recovery of cougar numbers to previous levels. Logan's (2001) research in New Mexico indicated that when harvest of the adult cougars exceeds 28% a population decline occurs. The 44% annual harvest level on Big Creek exceeded that threshold, and age structure on harvested cougars has changed from primarily mature cougars to mostly subadults (Idaho Department of Fish and Game unpublished data, McCall, Idaho, USA)..

Intraspecific strife was not observed during previous cougar research projects in this study area (Hornocker 1970, Seidensticker (1973). Seidensticker (1973) mentioned that male cougars he handled on Big Creek did not have scars from fighting. Hornocker (1970) suggested fighting should be rare in a stable cougar population. In contrast, we documented intraspecific strife among cougars in three cases of mature male cougars killing other males and we observed injuries and scars on males from fighting. Our findings were more similar to those of Logan et al. (1986), Murphy (1998), Ross and Jalkotzy (1992) and Ruth (2004b) and were indicative of a disrupted social structure. Ruth (2004b) suggested that increased intraspecific aggression among cougars may lend further support of exploitation competition between sympatric cougars and wolves in northwestern Montana. It is unclear whether this breakdown in social structure observed on Big Creek was precipitated by declining elk numbers, wolf arrival in the Big Creek drainage, or other factors, but the strife we observed occurred in the first two years of the study, prior to wildfire and heavy hunting pressure.

Interference competition can be difficult to quantify because it can occur at both individual and population levels (Ruth 2004b). Interference competition occurred on Big Creek when wolves adversely affected cougars when they visited cougar kills, usurped carcasses from cougars, and caused cougars to make long distance movements. These cougar responses could result in decreased food intake or starvation (Ruth 2004b) and increased physical and endocrine stress, and potentially decreased hunting success if cougars leave preferred hunting areas to avoid wolves. These factors could have contributed to the observed lower cougar reproductive success and survival on Big Creek, although Kunkel et al. (1999) believed that it was unlikely that interference competition by wolves resulted in an observed cougar population decline in Montana.

Conclusion

We found biological and social cougar responses that could be explained by interspecific competition with recently established wolves. Unfortunately, with confounding factors which can also affect cougar population dynamics - such as a declining prey population, high hunter harvest, large-scale environmental change from forest fire - it is difficult to assess the relative contributions of each factor in causing the observed decline in the cougar population and its productivity during the 1999-2002 study period. The combination of factors exacerbated the effects of interspecific competition. Wolves were more adaptable to large-scale environmental change than were cougars. Wolves are social animals so the wolf pack shared a very large home range. Therefore, the wolf pack was able to move long distances (35 km) within their home range to areas of higher prey density in another ungulate winter range when elk abandoned the burned Big Creek winter range after the fire. In contrast, cougars were limited by their smaller home range sizes from moving long distances to more suitable areas. When elk left the burned Big Creek winter range the first winter after fire, cougars responded to the lower prey density by diversifying their diets. Branch et al. (1996) observed a similar response by cougars in Argentina following a prey population decline. Wolves benefited more from their association with cougars than cougars did with their association with wolves, since wolves gained food from cougars more often. The timing of this study immediately after wolf reintroduction allowed us to examine cougar and wolf responses to "first encounters" with each other. The characteristics of this initial phase of coexistence may be transient and more overt compared to a future time period when the two large carnivores will act to minimize the effects of interspecific competition by partitioning habitat, food resources, and/or space, or one species' population will decline as a result of interspecific competition.

ACKNOWLEDGEMENTS

Primary financial support was generously provided by the DeVlieg Foundation. Project Cooperators were the Hornocker Wildlife Institute–Wildlife Conservation Society, the University of Idaho, the Nez Perce Tribe, and the Idaho Department of Fish & Game. We thank our dedicated field assistants, including: Pete Armichardy, Andrea Bristol, Wes Craddock, Josh Holloway, Matt Jones, Chris McDaniel, Jay Mize, Mike Schlegel, and Renan Yanish. Ray Arnold piloted fixed wing aircraft used, and Jim Pope provided helicopter assistance.

LITERATURE CITED

Branch, L.C., M. Pessino, and D. Villarreal. 1996. Response of pumas to a population decline of the plains vizcacha. Journal of Mamma logy 77:1132-1140.

Boyd, D.K., and G.K. Neale. 1992. An adult cougar (*Felis concolor*) killed by gray wolves (*Canis lupus*) in Glacier National Park, Montana. Canadian Field-Naturalist 106:524-525.

Caswell, L.G. 1895. Diaries of L.G. Caswell, Idaho State Historical Library. Boise, ID. Unpublished MS 32/437. 48 pp.

Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Hooge, P.N., and B. Eichenlaub. 1997. Animal movement extension to ArcView: version 1.1 Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21. 39pp.

Husseman, J.S., D.L. Murray, G. Power, C. Mack, C.R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591-601.

Koehler, G.M., and M.G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mamma logy 72:391-396.

Kunkel, K. and D.H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65:520-530.

Kunkel, K.E., T.K. Ruth, D.H. Pletscher, and M.G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901-910.

Logan, K.A., L.L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648-654.

Logan, K.A., and L.L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC. 463 pp.

Murphy, K.M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. PhD Dissertation, University of Idaho, Moscow, ID. 147 pp.

Neiland, K.A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. Journal of Wildlife Management 34:904-907.

Quigley, H.B., G.M. Koehler, and M.G. Hornocker. 1989. Dynamics of a mountain lion population in central Idaho over a 20-year period. Third Mountain Lion Workshop, December, 1988. Prescott, Arizona.

Quigley, K. 2000. Hornocker Wildlife Institute immobilization and biological sampling protocols. Hornocker Wildlife Institute, Moscow, Idaho, USA.

Robinette, W.L., J.S. Gashwiler, and O.W. Morris. 1961. Notes on cougar productivity and life history. Journal of Mamma logy 42:209-217.

Ross, P.I and M.G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417-426.

Ruth, T.K. 2004(a). Ghost of the Rockies: the Yellowstone cougar project. Winter 2004, Yellowstone Science 12:13-24.

Ruth, T.K. 2004(b). Patterns of resource use among cougars and wolves in northwestern Montana and southeastern British Columbia. PhD Dissertation, University of Idaho, Moscow, ID. 122 pp.

Seidensticker, J.C. 1973. Mountain lion social organization in the Idaho Primitive Area. PhD Dissertation, Idaho Cooperative Wildlife Research Unit, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID. 146 pp.

Seidensticker, J.C., M.G. Hornocker, W.V. Wiles, and J.P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35. 60pp.