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Coyote Foraging Ecology, Vigilance, and Behavioral Cascades in Response to Gray Wolf Reintroduction in Yellowstone National Park

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COYOTE FORAGING ECOLOGY, VIGILANCE, AND BEHAVIORAL CASCADES

IN RESPONSE TO GRAY WOLF REINTRODUCTION

IN YELLOWSTONE NATIONAL PARK

by

T. Adam Switalski

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ABSTRACT

Coyote Foraging Ecology, Vigilance, and Behavioral Cascades

in Response to Gray Wolf Reintroduction

in Yellowstone National Park

by

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Utah State University, 2002

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Vigilance behavior can aid in the detection of predators and may also play a role in

observation of conspecifics, in food acquisition, and in the prevention of

kleptoparasitism. However, in most occasions, vigilance is most important as an anti-

predator function. Generally, factors that increase the risk of predation also increase the

amount of vigilance. We examined whether the reintroduction of the large predator, the

wolf, in Yellowstone National Park (YNP) would influence coyote vigilance and foraging

ecology. From December 1997 to July 2000, we collected 1743 h of coyote activity

budgets. Coyote home ranges occurred within wolf territories (termed high-use or non-

buffer zone areas) and also between them in buffer zones. In high wolf use areas as well

as when wolves were present, coyotes fed on carcasses much more; however, they

increased the amount of vigilance and decreased rest to prevent predation. Wolf kills

may provide a quick source of food and be energetically advantageous to coyotes; however, costs include increased vigilance, decreased rest, and a higher predation risk. Vigilance and avoidance behavioral responses to the reintroduction of large predators may ultimately be more common outcomes than actual killing by competing carnivores of prey. Keystone carnivore reintroductions have a variety of cascading effects throughout the ecosystem and can be driven by both numeric responses (trophic cascades) and behavioral responses ("behavioral cascades"). Behavioral cascades resulting from increased vigilance or spatial changes may lead ultimately to numeric changes and trophic cascades.   (56 pages)

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INTRODUCTION

Species extinction due to human population growth and subsequent loss of habitat has been predicted to be 100,000 times higher today than over the last few millennia (Wilson 1992). Large carnivores are at a particularly high risk of extinction because of their inherent rarity, large habitat requirements, cultural biases, and direct competition with humans for prey (Woodroffe and Ginsberg 2001). Accordingly, large carnivores have been extirpated from much of their range.

Large carnivores are considered keystone species, when they exert a disproportionately high influence on an ecosystem relative to their numbers (Power and Mills 1995). The loss of large predators can disrupt the stability of an entire ecosystem leading to further extinctions (Terborgh et al. 1999). The absence of large predators has led to large and significant changes in the abundance of certain prey and competing carnivore species. For example, the extirpation of wolves (*Canis lupus*) and cougars (*Felis concolor*) in the eastern forests of the U. S. has led to increased numbers of white-tailed deer (*Odocoileus virginianus*; McShea et al. 1997) and the expansion of the range of coyotes (*Canis latrans*; Mech 1970), who now have expanded their range to Newfoundland (Bissonette, pers. comm.). In addition to changing the distribution and abundance of prey and competing carnivore species, predators can influence their behavior as well. Berger (1998) argued that when specific predators are absent for generations, prey species lose their ability to recognize and avoid those predators or actively defend against them. Further, in the absence of predators, these species can be time maximizers and maximize fecundity by feeding for longer periods of time (Schoener

1971). These behavioral changes may have had cascading effects and ultimately changed entire ecosystems.

Reintroduction of large predators is being used to restore and promote biodiversity in previously disturbed ecosystems. For example, wolves have been reintroduced into several areas of the Rocky Mountains as well as North Carolina and are recolonizing many areas in the Midwest and along the Canadian border (Phillips et al. 1995; Mech 1995; Parsons 1998; Bangs et al. 2001). Preliminary results about the lethal impacts on prey populations are confounding (e.g., Kunkel and Pletscher 1999; Mech et al. 2001). However, reintroduced predators have reduced some competing carnivore populations (e.g., Crabtree and Sheldon 1999). Prey and competing carnivores appear to be quickly adjusting their behavior to coexist with reintroduced predators. Elk (*Cervus elaphus*) increased their vigilance and adjusted their space use allowing for coexistence, but as a result may have reduced their fitness because of decreasing amounts of time spent feeding and moving to suboptimal habitat (e.g., Laundré et al. 2001).

Vigilance behavior can aid in the detection of predators and may also play a role in observation of conspecifics, food acquisition, and in the prevention of kleptoparasitism (Quenette 1990). However, in most occasions, vigilance is most important as an anti-predator function. Generally, factors that increase the risk of predation also increase the amount of vigilance. Vigilance in mammalian carnivores has been observed in captive studies of meerkats (*Suricata suricata*; Moran 1984) and dwarf mongooses (*Helogala undulata rufula*; Rasa 1989), and in free-ranging cheetahs (*Acinonyx jubatus*; Caro 1987), eastern quolls (*Dasyurus viverrinus*; Jones 1998), polar bears (*Ursus maritimus*; Dyck et al. 2001), and coyotes (this study). Vigilance in ungulates has been much more

extensively examined with several studies in Southern Africa, Europe, and North America. Vigilance is influenced by a variety of environmental and social variables including group size, distance to refuge, position in the herd, body size, age, parenthood, habitat, predation pressure, and ecotourism. Increasing recognition and understanding of these factors may help us predict the effects of the reintroduction of keystone predators on their prey and competing carnivores.

One of the most frequently reported trends in behavioral ecology is that as group size increases, individual vigilance decreases (reviewed by Elgar 1989; Lima and Dill 1990; Roberts 1996; Frid 1997). These authors have posited two related hypotheses to explain this inverse relationship. First, as group size increases there are more eyes watching for predators, thus improving predator detection and requiring less vigilant time per individual. A second hypothesis stated that if the risk of predation is lowered with increasing group size, and vigilance is closely related to predation risk, then vigilance also should decrease with increasing group size. Roberts (1996), however, proposed a third alternative in which group size may be closely related to another confounding variable such as distance to cover, age, sex, observer proximity, density and type of food, time of day or season, presence of predators, position in group, and/or composition of group. Frid (1997) labeled this the "interactive factors hypothesis" in which the degree of vigilance depends on how other variables change predation risk. For example, in Dall's sheep (*Ovis dalli dalli*), the relationship between group size and vigilance decreased as the animal approached refugia (Frid 1997). Bissonette and Steinkamp (1996) found that California Bighorn sheep moved closer to cover when threatened.

Similarly, White et al. (2001) found that as yearling moose (*Alces alces gigas*) increased their distance from protective cover, vigilance increased.

Position in the herd also has been found to influence rates of vigilance. Animals in the center of the group have the advantage of animals on the periphery of the herd watching for predators, a statistically smaller chance of being singled out by the predator, and additional warning from the flight behavior of edge animals (Hamilton 1971; Bertram 1978; Dehn 1990; Burger and Gochfeld 1994). Consequently, the time spent in vigilance activities was much greater for ungulates on the edge of the herd in Spanish ibex (*Capra pyrenaica*; Alados 1985), pronghorn (*Antilocapra americana*; Lipetz and Bekoff 1982), and several African ungulate species (Underwood 1982; Bednekoff and Ritter 1994; Burger and Grochfeld 1994; Hunter and Skinner 1998).

Above a certain threshold, the risk of predation generally decreases as body size increases (Quenette 1990). Burger and Gochfeld (1994) reported that smaller species, including Uganda kob (*Kobus kob*) and impala (*Aepycerus melampus*), were more vigilant than intermediate-sized species, including wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), and cape buffalo (*Syncerus caffer*), while African elephants (*Loxodonta africana*) devoted almost no time to vigilance.

Juveniles may have higher levels of predation due to naïveté towards predators, decreased ability to escape attack, and incomplete development of anti-predator responses. A higher level of vigilance in juveniles than adults was reported for Spanish Ibex (Alados 1985), impala, and wildebeest (Hunter and Skinner 1998). White et al. (2001) reported more variation in rates of vigilance in juvenile moose, which may lead to greater mortality than in adults. Vigilance of mothers, in addition to reducing their own

risk of predation, may also help to reduce the vulnerability of juveniles. Accordingly, an increase in vigilance in lactating females has been shown in cheetah (Caro 1987), pronghorn (Lipetz and Bekoff 1982), several species of African ungulates (Burger and Gochfeld 1994; Hunter and Skinner 1998), and alpine ibex (*Capra ibex ibex*; Toïgo 1999).

Some habitats may expose animals to higher rates of predation than others. As a consequence, moose (Molvar and Bowyer 1994) and mule deer (*Odocoileus hemionus*; Altendorf et al. 2001) show higher levels of vigilance in riskier habitats than in safer habitats. The degree of predation pressure also influences vigilance behavior. When exposed to higher predation risk, elk (Laundré et al. 2001), impala, wildebeest (Hunter and Skinner 1998), and coyotes (this study) significantly increased their level of vigilance. Similarly, when the potential predator is physically present, eastern quoll (Jones 1998) and coyotes (this study) were more vigilant.

Finally, wildlife viewing and the vehicles used while observing may influence rates of vigilance. The effects of ecotourism on vigilance, however, have only recently been quantified. Polar bears (Dyck et al. 2001), grizzly bears (*Ursus arctos*; Owen Nevin, Utah State University, pers. comm.), wolves (pers. obs.), Asian rhino (*Rhinoceros unicornis*; Lott and McCoy 1995), and woodland caribou (*Rangifer tarandus caribou*; Duchesne et al. 2000) reduced the amount of time feeding and increased the amount of time being vigilant when in the presence of tourists.

In this thesis, we couple broad ecological studies with behavioral studies in an attempt to increase understanding of the effects of the reintroduction of wolves as keystone carnivores. We use the reintroduction of wolves into Yellowstone as a case study to

determine how coyotes are learning to coexist with this keystone carnivore. As early as 1937, Leopold addressed the effects of gray wolf presence (*Canis lupus*) on coyotes (*Canis latrans*). In his essay "Conservation in Mexico," Leopold questioned whether the absence of coyotes in the Chihuahuan mountains was a result of the presence of the once common Mexican wolf. Since then, several studies have addressed coyote-wolf coexistence. In 1957, when Mech began studying wolf ecology on Isle Royale, just 8 years after their colonization, coyotes had already been extirpated from the island. Mech (1966:160) postulated that wolves were responsible: "Since coyotes and wolves are closely related and since wolves are strongly territorial, it is not unlikely that on a limited range, such as Isle Royale, wolves would chase, and probably kill, every coyote encountered." Direct killing of coyotes by wolves has since been documented in Minnesota (Berg and Chesness 1978), Alaska (Thurber et al. 1992), Manitoba (Carbyn 1982; Paquet 1991a, 1991b, 1992), Montana (Arjo and Pletscher 1999), and Wyoming (Wigglesworth 2000). In many areas, however, coyotes and wolves are sympatric. Coyote and wolf coexistence can be facilitated through resource partitioning including spatial avoidance (Berg and Chesness 1978; Fuller and Keith 1981; Dekker 1989; Thurber et al. 1992; Paquet 1992), temporal separation (Carbyn 1982; Arjo and Pletscher 1999), or low degree of diet overlap (Thurber et al. 1992).

Historically gray wolves and coyotes were sympatric in Yellowstone National Park (YNP) (Murie 1940; Schullery and Whittlesey 1992). A federal predator removal program, established in 1872, succeeded in extirpating wolves from the park by 1933. For 60 years since that time, coyotes have thrived in Yellowstone without wolves. On January 12, 1995, 14 wolves were translocated from Canada and reintroduced into YNP.

An additional 17 wolves were reintroduced the following year. Their population increased quickly, and during 1996 and 1997 the wolf population had the highest fecundity recorded for the species (Smith 2000). By July 2000, there were 118 wolves within the Greater Yellowstone Ecosystem (GYE) (Smith et al. 2000). Today, the GYE supports at least 177 wolves (USFWS et al. 2001).

Gray wolves have been reintroduced into several areas of the Rocky Mountains as well as red wolves (*Canis rufus*) in North Carolina (Phillips et al. 1995; Bangs et al. 2001) and Mexican wolves into the American Southwest (Parsons 1998). Further, gray wolves are recolonizing many areas in the Midwest and along the Canadian border (Mech 1995). The consequences of these reintroductions are beginning to be understood (e.g., Clark et al. 1999). Additionally, wolves are dispersing from existing reintroduction sites and are being considered for further reintroductions into the Olympic Mountains of Washington (Ratti et al. 1999), Colorado (Bennett 1994), and the Northeastern United States (Mladenoff and Sickley 1998; Harrison and Chapin 1998). Coyotes are present in all of the proposed reintroduction sites for gray, Mexican, and red wolves, and in the areas to which they have dispersed.

Before the reintroduction of wolves into Yellowstone, researchers in other areas of North America rarely witnessed coyote-wolf encounters in the field. Since reintroduction, however, hundreds wolf-coyote interactions have been observed and recorded in YNP. Taking advantage of this natural experiment, we examined whether the reintroduction of wolves would influence coyote life history strategies by altering their time activity budgets. Gese et al. (1996a, 1996b) quantified coyote behavior in the Lamar Valley of YNP before wolf reintroduction, creating a benchmark for gauging the

effects of this top predator on coyote behavior. We are not aware of any study that has used direct observations to assess behavioral changes of coyote individuals caused by the reintroduction of wolves. Using direct observations in the Lamar Valley, we were able to quantify behavioral time budgets of coyotes in the presence of wolves. We addressed the following questions: (1) Do coyotes living between wolf packs ("buffer zones") exhibit different behavioral time budgets than coyotes living in high wolf use areas? (2) Now that wolves have become established in the Lamar Valley, do coyotes exhibit different behavioral time budgets when wolves are physically present (within the study area) than when they are absent (outside of the study area)?

STUDY AREA

We conducted research in the Lamar River Valley in the Northern Range of YNP, Wyoming ($44^{o}52$'N, $110^{o}11$'E). The study area encompassed the 70 km^2 study area delineated by Gese et al. (1996a, 1996b) and was extended an additional 30 km^2 west of Lamar Canyon into what is known locally as "Little America." The Lamar Valley is a high elevation, open river valley at approximately 2000m elevation and is bordered by very steep forested habitat to the south and more gradually rising, open sage-grassland habitat to the north. The climate in the study area is characterized by long, cold winters and cool summers (Houston 1982). Mean temperature is 1.8^{o}C and annual average annual precipitation is 31.7 cm, mostly falling as snow (Houston 1982).

Ungulate carcasses and small mammals are the main food source for coyotes in YNP. YNP is home to seven different species of ungulates, including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bison (*Bison bison*), moose (*Alces aces*), bighorn sheep (*Ovis canadensis*), and white-tailed deer (*Odocoileus virginianus*). Small mammals present in YNP included but were not limited to microtines (*Microtus spp.*), mice (*Peromyscus spp.*), northern pocket gophers (*Thomomys talpoides*), and Uinta ground squirrels (*Spermophilus armatus*).

METHODS

Each coyote was classified as either a member of a resident pack or as a transient.

Resident packs, including resident pairs, actively defended well-defined territories

whereas transients were not associated with any pack or area and exhibited nomadic

movements (modified from Bowen 1981). Pack sizes were determined through repeated

observations of animals displaying affiliative behaviors that included traveling and

resting together, as well as other social interactions. Based on observed dominance

hierarchies within each resident pack, individuals were classified as either alphas

(dominant breeding adult), betas (subordinate adults and yearlings), or pups (young of the

year) (Schenkel 1947, 1967; Rabb et al. 1967; Mech 1970).

From December 1997 to July 2000, we made observations of both radio-collared and

unmarked coyotes and wolves in the Lamar and Soda Butte Valleys of YNP.

Observations were made during daylight hours using 45x-spotting scopes. We recorded

wolf and coyote locations daily either by observations or with telemetry. We randomly

chose which coyote packs to observe before going into the field. We identified a series

of observation points from which each pack territory could be viewed. From these

observation points we attempted to locate the coyote highest on the priority list. If this

search was unsuccessful, we searched for the animal of next highest priority.

Once a coyote was located, we continuously recorded all activities of that animal using

focal animal sampling (Lehner 1979). Using Lotus 123, we recorded the types of

behaviors, as well as the time of day recorded. Simultaneously, we recorded travel routes

and behaviors on 7.5-minute quadrangle maps. Attributes of the focal animal, including

gender, social status, age class (adult, yearling, or pup), pack name, and pack size were

also entered into the spreadsheet. Identified behaviors (modified from Gese et al. 1996a,b) included (1) rest/alert: the coyote was sitting upright or lying down with head raised; (2) rest/sleep: lying down with head lowered; (3) travel: moving from one location to another; (4) hunting small mammals: the total time spent searching (looking or listening for prey) and orienting (looking listening toward a prey item), not including the amount of time spent traveling between predation attempts; (5) successful predation attempt: the coyote captured a prey item; (6) unsuccessful predation attempt: the coyote was hunting but was unable to capture the prey item; (7) feeding on carcass: the coyote was feeding on an ungulate carcass; (8) howling: any audible sound; (9) vigilance: the coyote looked repeatedly to distant stimuli, using visual and auditory senses; muzzle was elevated or level and not oriented toward the ground (as is the case in "orient"); this could occur while traveling, hunting, or feeding on a carcass; (10) other: the coyote performed behaviors not adequately described by the existing categories including: urination, defecation, and social intraspecific interactions both affiliative and agonistic. The behaviors categorized as "other" comprised <4% of the total activity budget. The observed behaviors were mutually exclusive and could be determined unambiguously by field personnel. We calculated the sum and frequency of each behavior using Statistical Application Software (SAS). We deleted from the sample any period of time when the focal animal was out of sight.

We determined coyote territories primarily through observations of activity and scent marking. Fig. 1 represents the Lamar Valley coyote territories averaged for the 3 years of the study. The Park Service determined wolf territories using aerial and ground-based telemetry of radio-collared individuals coupled with observations (Smith et al. 2000;

USFWS et al. 2001; Mech et al. 2001). Additionally, the National Park Service recorded snow depth and maximum and minimum temperature daily during the winter at the permanent weather station at the Lamar Ranger Station.

We used SAS for our statistical analysis. We followed a factorial (split-plot) design where season was the repeated measure (Littell et al. 1994). The sample unit was the individual coyote for all statistical analysis. We used analysis of variance (ANOVA) using proc mixed; least squared means are reported. We used the proportion of time each behavior was performed relative to their total time budget. For analysis, we identified three phenological seasons: dispersal/breeding (15 October – 15 February), gestation (16 February – 15 April), and pup rearing (16 April – 15 July). From 16 July to 14 October, no fieldwork was conducted due to low visibility in high grass.
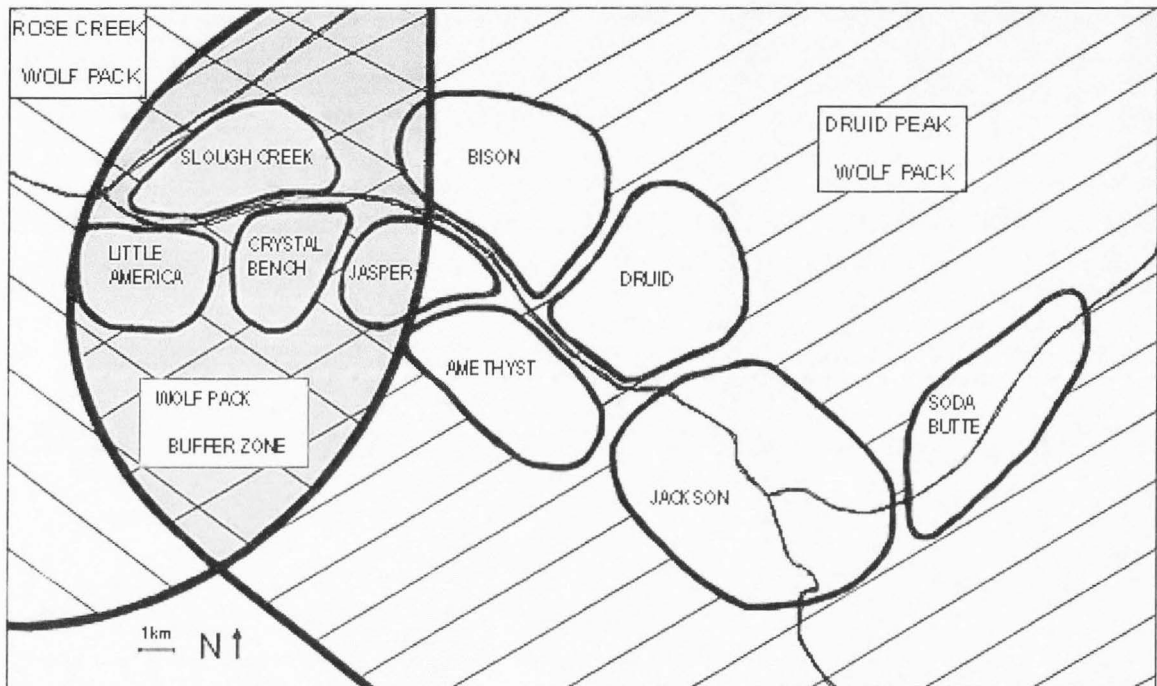
Fig. 1. Coyote and wolf pack territories including wolf "buffer zone" in the Lamar Valley in Yellowstone National Park, Wyoming, December 1997 to July 2000 (Modified from Smith et al. 2000, USFWS et al. 2001, Mech et al. 2001).

RESULTS

From December 1997 to July 2000, we made 1243 observations of coyotes and collected 1743 h of coyote activity budgets. We observed 28 resident coyotes from 9 packs, plus transients. Ten pack members were either radio-collared or implanted with radio transmitters, while 18 were identifiable only by distinctive physical characteristics. Of the known animals, 16 were male and 12 were female. We observed 24 alphas and 4 betas. We observed 3 members of the Soda Butte pack for 168 h, 4 members of the Jackson Ridge pack for 264 h, 4 members of the Druid pack for 201 h, 4 members of the Bison pack for 163 h, 2 members of the Amethyst pack for 156 h, 4 members of the Jasper pack for 98 h, 2 members of the Crystal Bench pack for 130 h, 2 members of the Slough Creek pack for 109 h, 3 members of the Little America pack for 106 h, and transients for 313 h.

Coyote Pack History

Since wolf reintroduction in 1995, the Lamar Valley coyote population has been reduced by an estimated 25-33% each winter (Crabtree and Sheldon 1999). Wolf predation appears to be the main cause of this decline. As of summer 2000, 9 packs with 24 adult coyotes remained in the study area (Fig. 1). Most coyotes documented killed by wolves were scavenging wolf-killed carcasses (Crabtree and Sheldon 1999).

Among the 9 packs studied, only 1 pack retained the same alpha pair during all 3 years of this study. All other packs experienced at least one alpha turnover. The Bison pack had a new alpha pair each year and the Jasper pack had a new alpha male twice during 2000. Wolf predation is assumed to be the main cause of the high rate of turnover;

however, actual predation of alphas was rarely witnessed. We witnessed a 13-year-old alpha female of the Druid pack killed by wolves in November 1998 and two members of the Amethyst pack were observed killed by wolves in February 1999.

The composition of each pack differed greatly from pre-wolf reintroduction observations by Gese et al. (1996a, 1996b). Large packs of coyotes with a dominance hierarchy, common before wolf reintroduction, are now rare. Pack size averaged 3.2 (range = 2.7-3.7) during our study, usually consisting of a breeding pair with a beta from the previous summer. Rarely did pups survive past their first year presumably due to high wolf predation and canine parvovirus.

Wolf Pack History

Two wolf packs, Druid Peak and Rose Creek, lived in the study area. The Rose Creek pack (n = 3) was introduced into the study area in January 1995 from Alberta, while the Druid Peak pack (n = 5) was introduced the following winter in January 1996 from British Columbia. After about 10 weeks in acclimation pens, the wolves were released and after an exploratory period settled into territories (Phillips and Smith 1997). During the length of the study, the Druid Peak pack lived in the Lamar and Soda Butte Valleys west to Slough Creek, encompassing most of the study area (Smith et al. 2000; USFWS et al. 2001; Mech et al. 2001; Fig.1). The Rose Creek pack territory was also very stable, ranging from the Lamar Canyon to Hellroaring Creek. The two wolf territories overlapped on the west side of the study area creating a buffer zone (Fig. 1, Hoskinson and Mech 1976; Mech 1977; Rogers et al. 1980; Lewis and Murray 1993). Fig. 1 shows only that portion of the 2 wolf packs that overlapped the coyote packs under study. Pack sizes ranged from 7-8 adults in the Druid Peak pack and 15-22 adults in the Rose Creek

pack during the length of the study (Smith et al. 2000; USFWS et al. 2001; Mech et al. 2001).

Territory use by wolves varied spatially during the course of the year (D. Smith, NPS, pers. comm.). During the gestation and pup-rearing seasons, the Druid Peak wolf pack denned and produced litters every year within the Soda Butte coyote pack territory. In spring 2000, however, a beta female from the Druid Peak wolf pack denned within the Amethyst coyote territory. She denned there only until mid-May and then, after the alpha female was killed, moved her pups to the historic den site. The Rose Creek wolf pack, however, denned toward the northern border of the Park and was outside the study area during most of the gestation and pup-rearing seasons. During the dispersal/breeding season, both packs were less localized and traveled, hunted, and made kills throughout the study area.

Environmental Conditions

The weather in Yellowstone varies greatly from year to year. Winter severity can influence reproduction, survival of young and old, and predation of ungulates (Houston 1982). To measure the annual variation in winter severity, we used an index of winter severity (IWS) that was calculated by combining snow water equivalent, accumulated minimum temperatures below the effective critical temperature of ungulates (temperature when animals must increase their metabolic rate to maintain adequate body temperature), and the availability of forage in the winter range (Farnes et al. 1999). According to the IWS for elk in the Lamar winter range, the winter prior to the beginning of this study (1996-1997) was the most severe since 1998 (Fig. 2). A midwinter rain event created a thick ice crust, resulting in large numbers of winter-killed ungulates. The first winter of
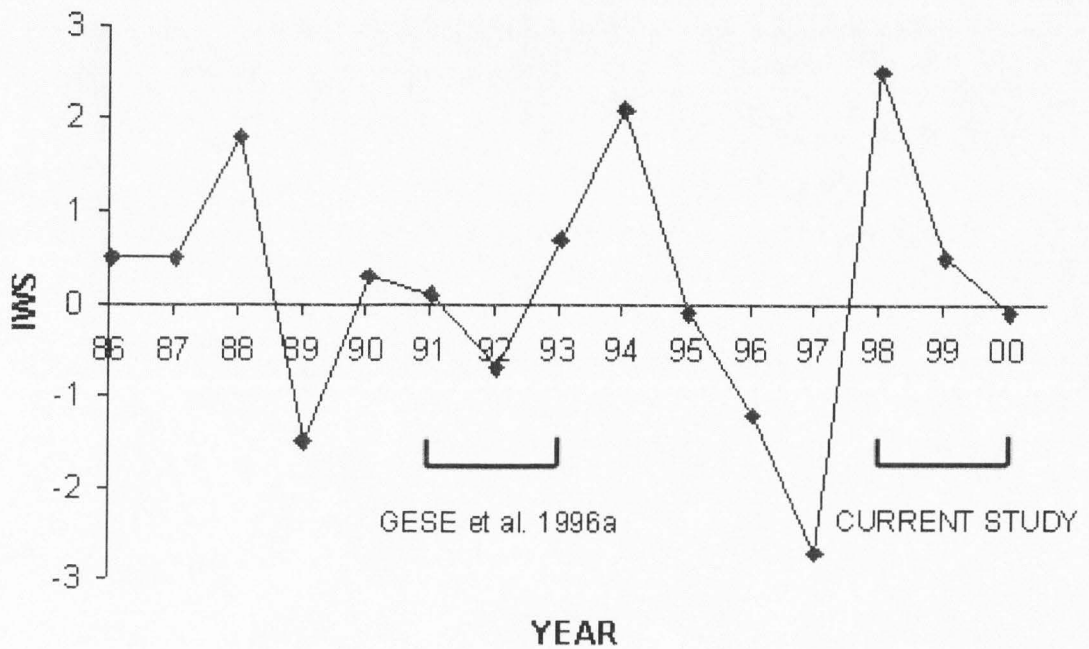
Fig. 2. Index of winter severity (IWS) for elk during the winters of 1986 to 2000 in the Lamar River Range in Yellowstone National Park, Wyoming (Modified from Farnes et al. 2000). Brackets indicate the years coyote behavior was observed prior to wolf reintroduction (Gese et al. 1996a) and after wolf reintroduction (current study).
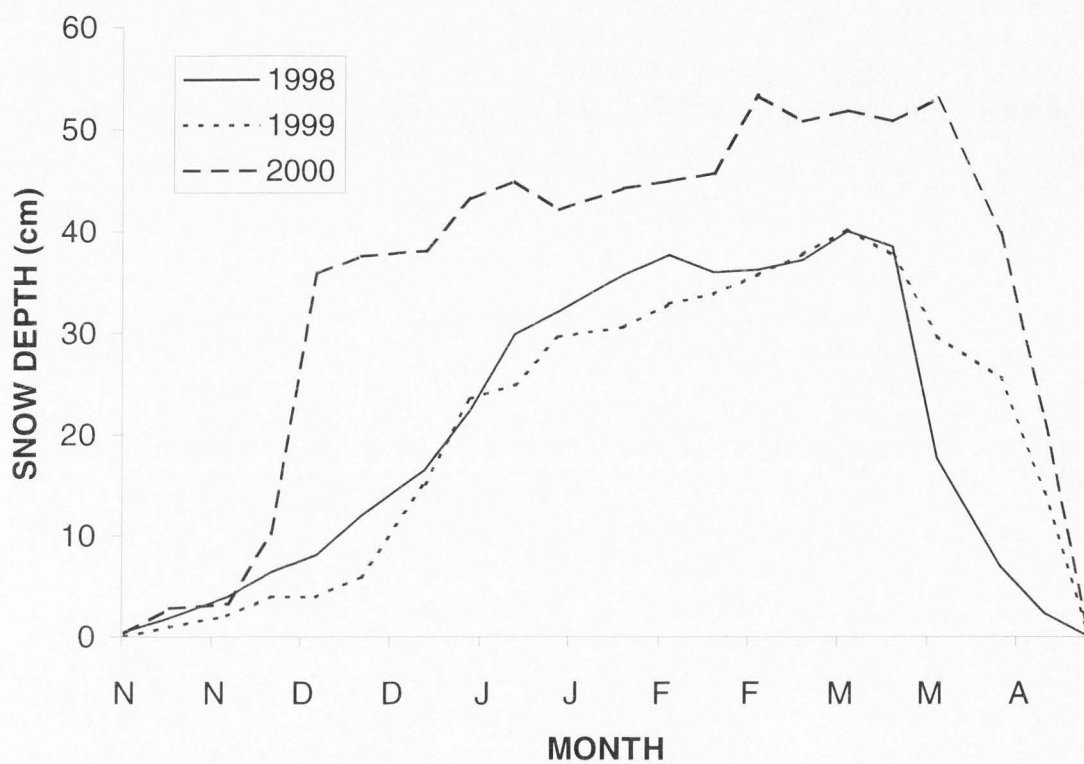
Fig. 3. Mean snow depth for each week during the winters of 1998, 1999, and 2000 in the Lamar Valley, Yellowstone National Park, Wyoming.

this study (1997-1998), however, was considered the mildest winter in decades. Snow depth reached a maximum of 41 cm and was >30 cm for only 64 days (Fig. 3). The second winter of this study was also relatively mild with snow conditions similar to the first winter. Snow depth reached a maximum of 40 cm and was >30 cm for 60 days. The third winter was the most severe of this study (1999-2000) and was characterized by early snowfall and deep snowpack. Snow depth reached a maximum of 66 cm and was >30 cm for 110 days.

In contrast to Gese et al.'s (1996a, 1996b) study from January 1991 to July 1993, there were very few winter-killed ungulates during this study, even though the degree of winter severity was similar during 1999 and 2000 (Fig. 2). During mild or moderately severe winters, the rate of wolf predation and wolf pack size now determined the amount of carrion available to coyotes (C. Wilmers, University of California-Berkley, in prep.). Generally, wolf predation increased in late winter (Smith et al. 2000; USFWS et al. 2001; Mech et al. 2001); however, ungulate carrion is now available to coyotes year round.

Coyote Activity Budgets

As expected, coyote activity budgets varied throughout the year (Fig. 4). Overall, coyotes decreased the amount of travel and hunting, and increased the amount of rest during the winter months. When the snow melted and ground squirrels emerged in mid-April, coyotes decreased the amount of time sleeping and increased the amount of time traveling and hunting. Contrary to Gese et al. (1996a), however, carcass use did not vary dramatically from November to July. In June most elk migrated from the valley to higher elevation summering grounds and we found few kills. During this study, vigilance did not appear to vary much throughout the year (Fig. 4).

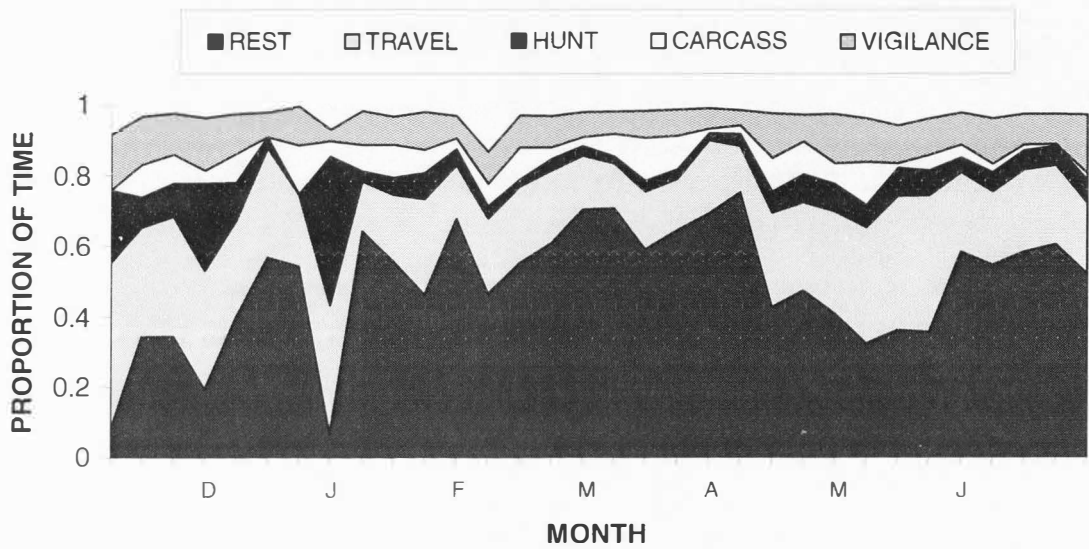**Fig. 4.** The proportion of time coyotes were observed to spend resting, traveling, hunting small mammals, feeding on carcasses, and vigilant each week from November to June during three field seasons (1998 - 2000) in Yellowstone National Park, Wyoming.

Effect of Level of Wolf Activity on Coyote
Activity Budgets

We wanted to determine if the degree of wolf activity influenced resident coyote activity budgets. Four coyote pack territories (Little America, Slough Creek, Crystal Bench, and Jasper) were located within the buffer zone between the Druid Peak and Rose Creek wolf packs (see Fig. 1). Wolves visited the buffer zone less frequently than other parts of their range and coyotes had fewer agonistic interactions with wolves.

We used a multi-way ANOVA and found a significant difference in the amount of time coyotes rested ($P = 0.02$), fed on carcasses ($P < 0.01$), and vigilance ($P < 0.01$) in the buffer versus non-buffer zones (Table 1, Fig. 5). Coyotes rested more (50% vs. 39%), fed on carcasses less (2% vs. 8%), and were less vigilant (9% vs. 14%) in the buffer zone than the non-buffer zone. We did not find a significant difference in the amount of time coyotes traveled and hunted for small mammals.

Coyote Activity Budgets in the Presence
and Absence of Wolves

The degree of wolf use influenced the activity budgets of coyotes, so we examined whether the actual physical presence of wolves had similar effects. Wolves were considered present if they were within the study area and absent if they were outside of the study area or on the opposite side of the study area from the focal coyote. We determined presence or absence by telemetry and observations of wolves. We realize that scent marks remained even when wolves were not present. When wolves were within the study area, coyotes could use visual cues to determine wolf presence. When wolves were distant from coyote home ranges, coyotes relied only on previous experiences and olfactory cues to make behavioral decisions. We had 398 observations where wolves

Table 1. ANOVAs showing the influence of snow depth, the degree of wolf activity, sex, and year (Model 1) and the influence of wolf distance, sex, and snow depth (Model 2) on the proportion of time coyotes spent in 5 behaviors in the Lamar Valley, Yellowstone National Park, Wyoming, December 1997 to July 2000.

Model 1		Rest		Travel		Hunt		Carcass		Vigilance	
Source	df	F	P	F	P	F	P	F	P	F	P
Wolf activity[a]	1	5.61	0.02	0.71	0.40	0.08	0.77	13.28	<0.01	12.98	<0.01
Sex[b]	1	1.17	0.29	3.87	0.06	1.63	0.21	0.33	0.57	2.74	0.11
Year[c]	1	0.03	0.87	0.11	0.74	1.97	0.17	1.60	0.21	4.54	0.04
Snow depth[d]	1	0.72	0.40	2.39	0.13	10.42	<0.01	13.57	<0.01	0.01	0.92
Wolf activity x snow depth	1	0.19	0.67	0.00	0.97	0.73	0.40	3.03	0.09	1.28	0.27
Sex x snow depth	1	0.20	0.66	0.05	0.82	0.09	0.76	0.56	0.46	0.69	0.41
Year x snow depth	1	1.72	0.20	0.30	0.58	0.47	0.50	3.54	0.07	10.23	<0.01

Table 1. Continued.

Model 2 Source	df	Rest		Travel		Hunt		Carcass		Vigilance	
		F	P	F	P	F	P	F	P	F	P
Wolf distance[e]	1	11.13	<0.01	1.69	0.20	0.00	0.97	4.20	0.05	12.54	<0.01
Sex[b]	1	0.60	0.44	3.31	0.08	0.44	0.51	0.77	0.39	0.53	0.47
Snow depth[d]	1	3.17	0.08	5.51	0.02	3.49	0.07	4.07	0.05	4.46	0.04
Sex x wolf distance	1	0.01	0.91	0.07	0.79	2.35	0.13	0.27	0.61	0.51	0.48
Snow depth x wolf distance	1	0.00	0.95	0.09	0.76	1.44	0.24	0.10	0.76	0.45	0.51

[a] Buffer zone (Little America, Slough Creek, Crystal Bench, and Jasper coyote packs) or Non-buffer zone (Amethyst, Bison, Druid, Jackson, and Soda Butte coyote packs)

[b] Male or female

[c] 1998 and 1999 combined or 2000

[d] Low/none (less than 30cm) or high (greater than 30 cm)

[e] Present (wolves were within the study area) or absent (wolves were outside of the study area or on the opposite side of the study area from the focal coyote).
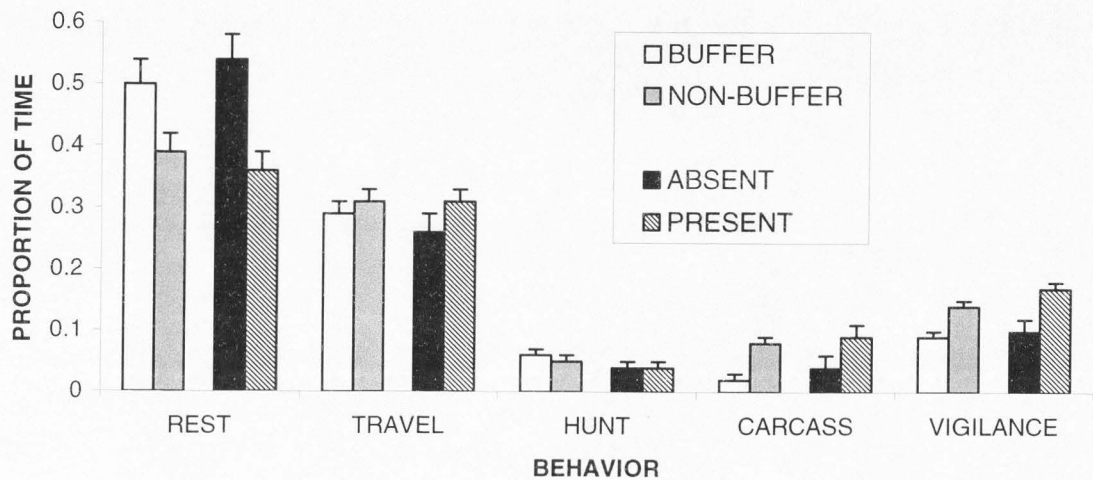
Fig. 5. The proportion of time resident coyotes were observed to spend resting, traveling, hunting small mammals, feeding on carcasses, and vigilant in the wolf buffer zone and non-buffer zone, and when wolves were physically present and absent (see text) in Yellowstone National Park, Wyoming, December 1997 to July 2000.

were present and 164 observations where wolves were absent. Due to our small sample size, we did not include yearly variation in our ANOVA model as in our previous analysis.

Coyotes exhibited different time budgets when wolves were present or absent (Fig. 5). We found a significant difference in the amount of time coyotes rested ($P < 0.01$), fed on carcasses ($P = 0.05$), and vigilance ($P < 0.01$) when wolves were present versus absent (Fig. 5). Coyotes rested more (54% vs. 36%), fed on carcasses less (4% vs. 9%), and were less vigilant (10% vs. 17%) when wolves were absent than when wolves were present. We did not find a significant difference in the amount of time coyotes traveled and hunted for small mammals when wolves were present versus absent.

DISCUSSION

Canid sympatry has been studied and is the topic of several reviews (Carbyn 1987; Litvaitis 1992; Peterson 1995; Johnson et al. 1996). However, because carnivores are rare, wide ranging, and difficult to observe, most studies have used telemetry and scat analysis to examine the diet, space use, habitat, and temporal overlap of these sympatric carnivores. The reintroduction of wolves into the Lamar Valley of YNP in 1995 allowed us to use direct observations to document what behavioral adaptations coyotes use to allow for coexistence with wolves. Our results show that coyotes in wolf buffer zones exhibit different behaviors than in the non-buffer zone. Additionally, when wolves are physically present, coyotes behave differently than when they are absent.

Although little winterkill was available during our study, we found that coyotes fed on carcasses throughout the year. This contrasts with Gese et al. (1996a) during a pre-wolf reintroduction study in YNP in which coyotes fed on winter-killed carcasses primarily from mid-December to March and relied on small mammals during the rest of the year. During our study, wolves in the Lamar Valley provided a continuous source of food for coyotes. The Druid Peak wolf pack had a pack size ranging from 7 to 8 adults during our study (Smith et al. 2000; USFWS et al. 2001; Mech et al. 2001) and provided a surplus of elk carrion for coyotes and other scavengers after the wolves apparently were satiated.

All of the coyote packs examined in this study were within the territories of the Druid Peak or Rose Creek wolf packs. Several of the coyote pack territories were located within the overlap between the wolf territories. Wolves tend to avoid intraspecific interactions in the areas where their home ranges overlap with other wolf packs, creating a "buffer zone." Wolf buffer zones have been found to have higher deer survivorship

(Hoskinson and Mech 1976; Mech 1977; Rogers et al. 1980; Lewis and Murray 1993) and provide refuge for coyotes (Berg and Chesness 1978; Fuller and Keith 1981; Arjo and Pletscher 1999). Similarly, red foxes (*Vulpes vulpes*) that occur sympatrically with coyotes disproportionately use the periphery of coyote home ranges (Voigt and Earle 1983; Major and Shelburne 1987; Sargeant et al. 1987; Harrison et al. 1989; Fuhrmann 1998). Coyotes living in the buffer zone between the Druid Peak and Rose Creek wolf pack territories within our study area had fewer agonistic interactions with wolves. In non-buffer areas, however, coyotes had more frequent encounters with wolves, and accordingly exhibited different behaviors than coyotes within the buffer zone.

Prior to wolf reintroduction, Gese et al. (1996a) did not find a significant difference in the amount of time different coyote packs rested or fed on carcasses. Our results, however, suggest that coyote packs within the buffer zone fed on carcasses less and rested more than coyote packs in the high wolf use non-buffer zone. The short amount of time spent feeding on carcasses was probably due to the lack of wolf-killed elk in the buffer zone. In the non-buffer zone, coyotes slept less possibly because they were wary of potential predation by wolves and could easily be killed if found sleeping. Similarly, when wolves were physically present, coyotes fed on carcasses much more and rested much less than when wolves were absent.

Predation plays a major role in natural selection and in the evolution of the ecology and behavior of animals (Dawkins and Krebs 1979). Predators kill large numbers of both prey and competing species and in some cases can be the leading source of mortality (Caro and Fitzgibbon 1992; Palomares and Caro 1999). Interspecific killing of coyotes by wolves has been well documented (Berg and Chesness 1978; Carbyn 1982; Paquet

1991a, 1991b, 1992; Thurber et al. 1992; Arjo and Pletscher 1999; Wigglesworth 2000).

In addition to wolves, cougars prey upon coyotes, and pups are preyed upon by golden

eagles.

"Naïve" prey and competing carnivore populations may reduce their vulnerability to

reintroduced predators through behavior changes. Behavioral responses may include

minimizing encounters with predators and/or decreasing the success of the attacking

predator (Endler 1986; Caro and Fitzgibbon 1992). These species can reduce encounters

with predators by adjusting their spatial or temporal use patterns. For example, when

reintroduced wolves hunted near the National Elk Refuge in Wyoming, elk routinely

dispersed to other feeding grounds, where they congregated in larger numbers and may

have had better visibility and warning of approaching predators (USFWS et al. 2001).

Additionally, coyotes in NW Montana spatially and temporally avoided wolves, became

more nocturnal, and avoided high wolf use areas seasonally (Arjo and Pletscher 1999).

If prey and competing carnivores remain in risky areas, they can lower the success rate

of attacking predators by scanning the environment. Many predators rely on surprise for

a successful attack and early detection by a potential victim of predation may allow for

escape. This vigilance behavior can aid in the detection of predators and may also play a

role in observation of conspecifics, food acquisition, and in the prevention of

kleptoparasitism (Quenette 1990). However, in most occasions, vigilance is most

important as an anti-predator function. Generally, factors that increase the risk of

predation also increase the amount of vigilance.

While feeding on carcasses, coyotes were at greatest risk of predation from wolves

and were often chased off the carcass. In fact, most coyotes we observed to be killed by

wolves were scavenging wolf-killed carcasses. Accordingly, coyotes were most vigilant while feeding on carcasses. Vigilance related to anti-predator behavior in mammalian carnivores has been observed in meerkat (*Suricata suricata*; Moran 1984), cheetah (*Acinonyx jubatus*; Caro 1987), dwarf mongoose (*Helogala undulata rufula*; Rasa 1989), and eastern quoll (*Dasyurus viverrinus*; Jones 1998). Vigilance in these carnivores has been shown to reduce predation risk; however, the amount of time available for foraging is also reduced. In the extreme, dwarf mongoose may be vigilant for 20 to 35% of their total possible foraging time (Rasa 1989).

Coyotes within the buffer zone were less vigilant than those in the non-buffer zone. Similarly, when wolves were absent, coyotes were less vigilant than when they were present. This suggests that clearly coyotes are using vigilance to detect wolves and when exposed to wolves are quickly learning to adjust their behavior to avoid wolf predation. Coyotes use 9% of their overall time budget being vigilant and as much as 14% in the high-risk non-buffer zone.

Typically, when we observed coyotes in the presence of wolves, the wolves had just made a fresh kill. After gorging themselves with meat, the wolves would usually bed down within a couple hundred meters of their kill. Waiting coyotes would almost immediately approach the carcass and begin feeding. Typically, once the wolves were satiated, they became more tolerant of scavenging coyotes and only occasionally defended their carcasses. Peterson (1995), however, proposed that this behavior may not be actual tolerance but the reduced ability of wolves with a full stomach to catch and kill the more agile coyote.

There appears to be a trade-off between vigilance and feeding. In high wolf use areas as well as when wolves were present, coyotes fed on carcasses much more; however, they increased the amount of vigilance to prevent predation. The degree of carrion available to coyotes may be related to wolf pack size, and as pack size increases, a threshold may be reached in which wolf kills will provide little energetic benefit to coyotes and other scavengers. Wolf kills may provide a quick source of food and be energetically advantageous to coyotes; however, costs include increased vigilance, decreased rest, and a higher predation risk. Predation is a major selecting force, however, and surviving coyotes have quickly learned to increase their vigilance and decrease their rest when wolves are present or in high-risk areas.

Keystone carnivore reintroductions may have a variety of cascading effects throughout the ecosystem and can be driven by both numeric responses (trophic cascades) and behavioral responses ("behavioral cascades"). When top predators were removed or reduced from North America, certain prey species populations became unnaturally high. The reintroduction of wolves into Yellowstone, for example, has been predicted to reduce the population of the dominant prey species, resulting in an increase in populations of competing, less vulnerable herbivores (Singer and Mack 1999). Alternatively, elk could buffer wolf numbers at high levels, thus rare ungulates could be in jeopardy (see Kunkel and Pletscher 1999). Reduction of prey populations may not only influence other species of the same guild, but among other trophic levels as well.

The relationship between wolves, moose, and vegetation has been examined extensively on Isle Royale in Michigan. During periods when the wolf population was

high (1975-1980), moose were taken more frequently and their population was reduced.

The reduction in moose population lowered browsing pressure on balsam fir and allowed

for increased growth of the tree (McLaren and Peterson 1994). However, when wolf

numbers were low and the moose population recovered (1982-1988), balsam fir was

eliminated where it occurred at low density (Brandner et al. 1990). Thus, wolves on Isle

Royale, through trophic cascades, influenced not only moose populations, but also the

vegetation that they fed on.

In Yellowstone, although there has been no measurable population change in elk,

behavioral changes of elk alone may result in similar cascading effects. Cow elk

appear to be avoiding high wolf use areas and foraging in other areas. This

displacement of elk has resulted in vegetative changes in Yellowstone, including the

recovery of aspen (*Populus tremuloides*; Ripple and Larsen 2000; Ripple et al. 2001)

and willow (*Salix* spp.). Further, these vegetative changes may result in higher

diversity of songbirds, increased numbers of amphibians, and recolonization of

beavers (*Castor canadensis*). Behavioral cascades seem to be the driving force

behind these effects.

Many competing carnivore species also have expanded their population and

distribution following the extirpation of large carnivores. Soulé et al. (1988)

proposed that when top carnivores are absent, mesopredators can become hyper-

abundant and can influence the entire community. This "mesopredator release" has

shown that the reduction of coyotes has increased native and exotic mesopredators,

thus increasing predation on certain bird species (Rogers and Caro 1998; Crooks and

Soulé 1999). Following the extirpation of wolves in Yellowstone, coyotes increased

their population size. Singer and Mack (1999) predicted that a decrease in the number of coyotes following wolf reintroduction could result in a trophic cascade by increasing the number of small mammals, and thereby leading to more food for badgers (*Taxidea taxus*), weasels (*Mustela* spp.), and foxes (*Vulpes vulpes*).

We propose that localized behavior changes in coyotes, including an increase of carcass use and avoidance of high wolf use areas, may be responsible for localized changes in small mammal abundance. We found an increase in the number of Uinta ground squirrels (*Spermophilus armatus*) in high wolf use areas (unpublished data). Although wolves will supplement their prey with small mammals during the summer (Murie 1944; Mech 1970; Carbyn and Kingsley 1979; Fuller 1989), we predict that prey populations of small mammals should locally increase in the near future. These results, however, may be confounded by environmental variables such as snow depth that have been found to greatly influence squirrel population density (Slade and Balph 1974).

Behavioral changes from increased vigilance may reduce overall fitness of certain prey species. An increase in vigilance in elk (Smith and Berger 2001; Laundré et al. 2001) and moose (Berger et al. 2001) has been observed since wolf reintroduction in 1995. For example, Laundré et al. (2001) predicted that increased vigilance in elk may ultimately lead to reduced fat content and lower body mass of females, lower survival rates during the winter and other stressful periods, as well as calves being born at lower weights. Increased vigilance in response to predators coupled with a decrease in the number of helpers at the den may also influence competing carnivores such as coyotes by reducing the survival of pups. Reduction in fitness and/or recruitment leads to decreased

population levels with associated ecosystem effects. Thus, behavior changes can result in

a numerical response of prey and be a driving force behind trophic cascades. Whether

the driving force is behavioral or from lethal predation, reintroduction of large keystone

carnivores may have wide-ranging effects throughout the ecosystem.

CONCLUSION

In conservation biology, behavioral studies are becoming increasingly important (Caro 1999). Reintroductions of keystone carnivores are proving to be a vital management tool to protect biodiversity, and behavior studies help to elucidate the effects of the restoration of these large predators. Documenting how species respond to the reintroduction of keystone carnivores will be essential in order to gain biological, social, and political justification for further reintroductions.

Prey and competing carnivores have been predicted to decline following the reintroduction and recolonization of large predators; however, preliminary results are conflicting. Recolonizing wolves appear to have reduced prey numbers in northwest Montana (Kunkel and Pletscher 1999), but there has not been a measurable decrease in prey populations in Yellowstone National Park (YNP) following wolf reintroduction (Mech et al. 2001). Further, wolves recolonizing the Upper Midwest do not appear to have reduced their prey populations (Minnesota DWR 2001; Wisconsin DNR 1999). However, wolves have influenced some competing carnivore populations. Wolves reintroduced into YNP have reduced coyote numbers (Crabtree and Sheldon 1999) and surviving coyotes have adjusted their behavior (this study).

The degree of wolf use and wolf presence influenced coyote behavior. Coyote packs within a buffer zone between the Druid Peak and Rose Creek wolf packs fed on carcasses less and rested more than coyote packs in the high wolf use non-buffer zone. Similarly, when wolves were physically present, more carrion were available and coyotes fed on them much more and rested much less than when wolves were absent. Additionally, coyotes within the buffer zone were less vigilant than those in the non-buffer zone.

Likewise, when wolves were absent, coyotes were less vigilant than when they were present. Thus, the degree of impact of wolves on coyotes varies spatially and temporally and coyotes in wolf buffer zones may be less impacted than in high wolf use areas, e.g., dens and rendezvous sites.

Coyotes appear to be benefiting energetically from wolves. Coyotes feed more on carcasses now that wolves are present in YNP. This shift in behavior is certainly due to an increase of available carrion from wolf kills. However, the degree of carrion available to coyotes may be related to wolf pack size, and as pack size increases, a threshold may be reached in which wolf kills will provide little energetic benefit to coyotes and other scavengers. Today there are 38 wolves in the Druid Peak wolf pack and now even bison carcasses are completely consumed by the wolf pack (pers. obs.).

Predation is playing a major selecting role, and surviving coyotes have quickly learned to increase their vigilance to detect wolves. Although wolf kills provide a quick source of food and are energetically advantageous to coyotes, coyotes have increased costs associated with increased vigilance, decreased rest, and higher risk of predation. These are very dynamic times for coyotes in the Lamar Valley with a high rate of alpha turnover and low recruitment and it may take many years for this system to reach a more stable equilibrium.

Nonlethal behavioral responses may ultimately be more important than lethal effects. Prey and competing carnivore species are adjusting their behavior and are showing increased vigilance. Additionally, there is some evidence that these species may be restricted to suboptimal habitat. Vigilance and avoidance behavior may be the primary reasons why there has not been a reduction in ungulate species and why

competing carnivore populations may still persist following wolf reintroduction in YNP. Quantifying the degree of vigilance necessary for coexistence is confounded by many social and environmental variables. Group size, distance to refuge, position in the herd, body size, age, parenthood, habitat type, predation pressure, and ecotourism may all influence the degree of vigilance, and should be considered in the management these species.

Keystone carnivore reintroductions are proving not only to influence their prey and competing carnivores species, but also to have many complex indirect cascading effects that are just beginning to be quantified. Although there are few terrestrial examples of trophic and behavioral cascades, it is evident that they are closely linked. Behavioral cascades resulting from increased vigilance or spatial changes may lead ultimately to numeric changes and trophic cascades. Whether the driving force is a change in behavior or from lethal predation, reintroduction of large keystone carnivores may have wide-ranging effects throughout the ecosystem.

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