

The Ecological Role of Coyotes on Yellowstone's Northern Range

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Adolph Murie's pioneering work on the ecology of coyotes (*Canis latrans*) in Yellowstone National Park, published in 1940, was a landmark of predator research in North America. By the late 1980s, biologists had undertaken long-term studies of other ungulate-killing carnivores such as grizzly bears and mountain lions, but not coyotes. In response to the fires of 1988 and in anticipation of gray wolf restoration, we undertook an intensive long-term study of coyotes on the northern range of Yellowstone National Park (YNP). From loose pairs to packs of 10 individuals, the coyote displays many of the behavioral characteristics seen among the 35 species within the family Canidae. Coyotes are an instructive group with which to examine the community structure of carnivores because of their variable social behavior, wide distribution, and ability to thrive in diverse environments.

History and Background

Coyotes, wolves, and red foxes all occur naturally in the greater Yellowstone ecosystem (GYE) and the northern range of the park. Schullery and Whittlesey (1992), who reviewed historical records of canids prior to 1890, found that while sightings of wolves and fox were common, coyote sightings were rather infrequent. Although this could be in part because coyotes were classified as wolves, several park officials were very adept at distinguishing species, even color morphs of red foxes. The lack of coyote sightings is in sharp contrast to the recorded take of predators from 1906 to 1927, when the last wolves were extirpated from the northern range. While 127 wolves and 134 mountain lions were



killed, a staggering 4,352 coyote mortalities were recorded. Could wolves have suppressed coyote numbers? When released from wolf pressure, could coyotes have quickly rebounded?

To address these questions and others regarding fire, weather, prey relations, and potential competitive interactions, an intensive study was needed—one that described and quantified the basic eco-

logical role of coyotes in YNP.

Our Study Begins

We initiated studies of the coyote on Yellowstone's northern range in 1989, six years prior to wolf restoration. Two study areas, the Lamar Valley and Black-tail Plateau, were chosen because of their differential patterns of burn from the 1988



Left: Jennifer Sheldon returns a coyote pup to its den after capture. Right: Jennifer Sheldon and Bob Crabtree simultaneously radiotrack coyotes and wolves in Lamar Valley.

fires, and because their topography allowed direct observation of coyote behavior in addition to use of fixed station radio-telemetry. Our goal was to maintain one to three radio-tagged adults in all territorial packs in both study areas in order to investigate spatial organization, estimate social class-specific demographic parameters (e.g., survival and reproduction), and enhance behavioral observations. Analysis of territoriality as well as the social and spatial system of coyotes requires identification of all coyotes in a given area (Moorcroft et al. 1999). Adult coyotes were captured with padded, offset, leg-hold traps that had attached tranquilizer tabs and other modifications to minimize injury and capture of non-target species. Coyote abundance was determined from mark-recapture estimates and direct counts (Crabtree et al. 1989).

We collected data on the sex, weight, condition, dentition, presence of scars and unique marks, and description of mammae for each coyote captured. To estimate age, we extracted the vestigial first premolar from an anaesthetized lower jaw. Blood samples were taken for serological analysis and DNA fingerprinting. Each adult coyote was ear-marked and fitted with a radio collar (functional for three to four years) that weighed less than 3 percent of each coyote's body weight. The proportion of breeding females in the population was estimated from activity and movement data during whelping.

Litter size was determined from den counts and by counting embryos from female carcasses. Pups were hand-captured at dens when 9 to 12 weeks old and surgically implanted with intraperitoneal radio-transmitters to allow estimates of early pup mortality, dispersal, and social interactions. Pups were intensively monitored during the summer months, the period of highest neonatal mortality, and later followed for as long as they were on the study area.

Both marked and unmarked coyotes were intensively observed in the Lamar study area with the aid of spotting scopes and radiotelemetry. Behavioral data (Gese et al. 1996a) were recorded on a handheld computer and locational data was mapped. Behavioral time budgets were developed from systematic observations made from hillsides located throughout the Lamar Valley. In the Blacktail study area, radio-tagged coyotes were intensively radiotracked but were not readily observed because of the undulating topography. Pack size was determined by repeated counts of known adults during winter. Effective group size (or social cohesiveness) was determined from the number of adult coyotes seen traveling together during morning transects.

Estimates of the annual biomass in take of various prey species by coyotes were primarily based on scat analysis. Scats were collected from predetermined transects in both the Lamar and Blacktail areas during winter, spring, summer, and

fall collection periods, and seasonal estimates of the fresh weight of prey consumed took into consideration the different rates at which different types of prey are digested by the coyote. A concurrent study of small mammal communities done from 1990 to 1994 provided estimates of availability and overall predation rates on small mammal prey.

Prior to the restoration of wolves we captured and radiotagged 67 adult coyotes and 62 pups between the fall of 1989 and spring of 1993. Adults were monitored seasonally for a total of more than 200 coyote-years. An additional 37 adult coyotes without collars were monitored in the Lamar Valley. The natural distinguishing marks of their pelage made individual identification and observation a viable study method.

The Social System of Coyotes

Coyotes exhibit a well-defined social system similar to that of gray wolves. Coyote packs on the northern range averaged six adults each during the winters of 1990–95, before wolves were reintroduced (Fig. 1). In 1993, the Bison Peak pack in the Lamar Valley included 10 adults plus a double litter, with two mothers producing a total of 12 pups. Coyote packs this large had not previously been described; however, nearly all other field studies have been conducted on coyote populations subjected to substantial levels of human exploitation, which signifi-

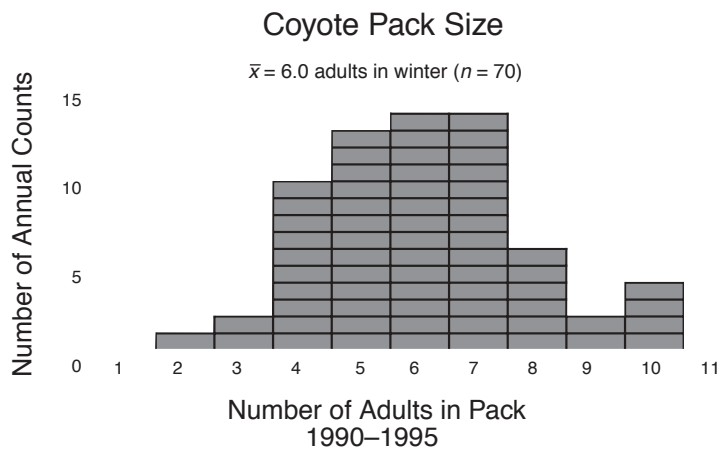


Figure 1. Prior to wolf reintroduction, coyote packs on the northern range had an estimated average of six adults each.

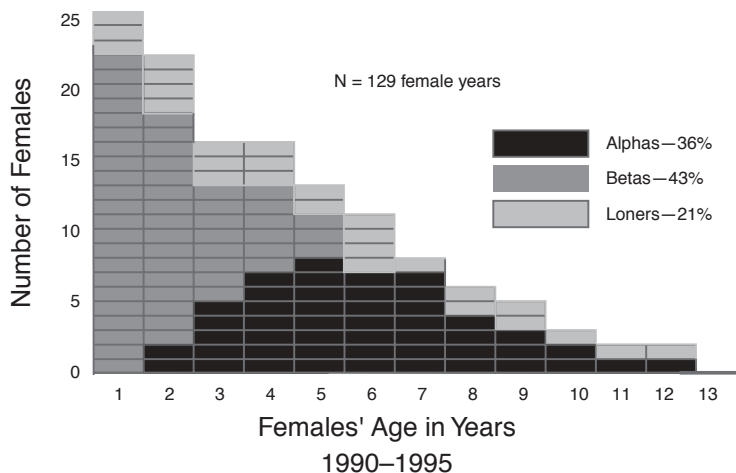


Figure 3. Estimated age distribution of female coyotes on the northern range.

cantly lowers pack size, and this has biased assumptions made about coyote demography and social behavior. The reason for such large packs in Yellowstone is related to the abundant prey (rodents and carcasses) and the fact the Yellowstone coyotes are protected from hunting and trapping. Research in Yellowstone and other protected areas (Crabtree 1989) has resulted in the coyote being viewed as a social canid similar to other medium and large-sized canids elsewhere in the world (Sheldon 1992).

Similar to gray wolves, coyotes live in territorial packs that consist of a dominant “alpha” breeding pair and subordinates, or “betas”—pups born in the current or previous years. Of the 104 adult coyotes we monitored, 88 percent be-

longed to packs; 30 percent were alphas and 58 percent were betas. Some betas were considered “slouches” because they did not help raise their younger siblings at the den. And although coyote pack members occupy the same territory and socialize often, they rarely travel all together. We found that 65 percent of our coyote observations on the northern range were of single coyotes (Fig. 2).

The remaining 12 percent of the coyotes residing in our study area were loners that did not belong to a pack and occupied the periphery of or spaces between territories. More than 85 percent of the loners were generally considered “nomads,” usually young coyotes who had low site fidelity and ranged over large areas from 50 to 300 km², presumably in

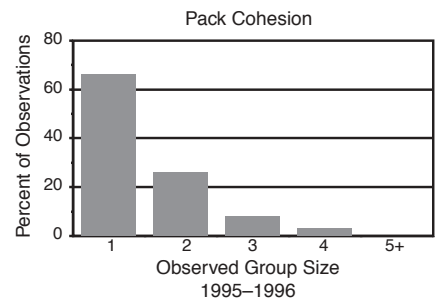


Figure 2. Unlike wolves, coyote pack members often travel alone.

search of a mate and a territorial vacancy. The other loners, considered “solitary residents,” were either “floaters” or former alphas. The floaters tended to be younger, age 1 to 3 years, showed weak fidelity to an area, and ranged over a larger area than the former alphas; they spent substantial time on the periphery of several territories and were suspected of being outcasts of one of the adjacent territories. Former alphas were age 3.5 to 11.5 years, and often had head and facial scars.

Reproduction

The average age of the coyotes we captured (excluding pups in the fall) was 3.8 years, the oldest average age yet reported in a field study. Even though females are physiologically capable of breeding by 10 months of age, especially in hunted or trapped populations, we found that with few exceptions, only the alphas (about 36 percent of the females in the study population, Fig. 3) successfully reproduced. Female coyotes have one estrous period each year, and the alphas generally mate in early February. In lightly exploited or unexploited areas like Yellowstone, females attain alpha status and

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initiate reproduction at 2 to 5 years of age. We found that the probability of a successful litter decreased starting around age seven. Although they failed to reproduce 14 percent of the time and sometimes lost entire litters shortly after birth, older alpha females still defended their territories and retained their alpha status.

Pregnant females begin to prepare for birth in late March and typically excavate two or three den sites originally dug by badgers. Alpha males are very attentive at this time and will bring food to their pregnant mates. Birth, or “whelping,” occurs in early April, when females spend the first week almost entirely underground, frequently nursing and grooming their pups. Other pack members guard the den site from enemies—bears, eagles, wolves, and other coyote packs. The pups are nursed exclusively by their mother until about mid-May, when they first emerge from their dens. At this time, the alpha male and beta pack members increase their guarding behavior and begin to regurgitate food for the pups.

Prior to wolf restoration, den emergence counts in late May averaged 4.4 pups per territory (Fig.4). However, indirect evidence suggested that approximately one pup per litter was lost in the first month after birth, resulting in an estimated litter size of 5.4 pups per territory at birth. Average annual litter size per territory varied greatly, from 2.6 pups per territory in 1994 to 6.9 pups in 1992. This is the greatest variation yet reported in a coyote population not affected by human exploitation. The sex ratio of pups, determined in June at the time of capture,

was 34 males to 28 females.

Similar to wolves, coyote packs occasionally produce a double litter. We have observed this five times in Yellowstone and estimate that double litters occur about 5 percent of the time. In one case, an 11-year-old alpha female had seven pups together with her daughter, a 2-year-old beta who had a litter of five pups. All pups were communally nursed and reared. The beta had been a den helper the previous year and appeared closely associated with her alpha mother.

When Hatier (1995) examined the role of helping behavior in 1992 and 1993, she found that in larger packs—those with more betas—more food was brought to the den and the breeding alpha pair spent significantly less time guarding it. Although an increase in the number of feedings (presumably because there were more betas) was significantly correlated with larger litter size, the overall pack size was not positively correlated with litter size or litter survival. Hatier suggested that these data support the contention that betas were tolerated by the alphas because they relieved the stress of reproduction (feeding and guarding) and because there were abundant food resources to support them.

Pup Survival

High neonatal pup mortality was observed from mid-June through mid-August each year. The summer survival rate, estimated from 62 radio-tagged pups captured each June 1990-1993, averaged 30 percent. The fall survival rate was much

higher—85 percent of the pups that survived the summer were still alive in the fall. Thus, given the average litter size of 4.4 pups emerging from the den, the average overall population productivity was only 1.5 pups surviving per pack per year.

The principal causes of pup mortality were disease and starvation, which occurred immediately after pup weaning in July and August. Examination of 18 pups recovered shortly after death revealed acute enteritis, a condition associated with an active parvovirus infection. Live parvovirus was cultured from tissue samples taken from one pup just after its death, which was associated with extended periods during which the maximum daily temperature reached 85° F or higher. Although the cause of death could not be determined for another 11 pups recovered at various stages of decomposition, all but one were found in or near water or a moist, shaded area, as were all of the 18 pups examined shortly after death. Pups infected with parvovirus become severely dehydrated and travel to water or wet shaded areas. Based on disease investigations by veterinarian Mark Johnson, and given the highly infectious nature of parvovirus, we suspect that all pups in an affected litter become infected; only the strongest (probably dominant) pups survive.

During the pre-wolf period (1990–1995), if a coyote pup survived for four months, its chances of becoming a mature adult were good. The overall annual survival rate for adult coyotes on the northern range was 91 percent and did not differ significantly between years. The

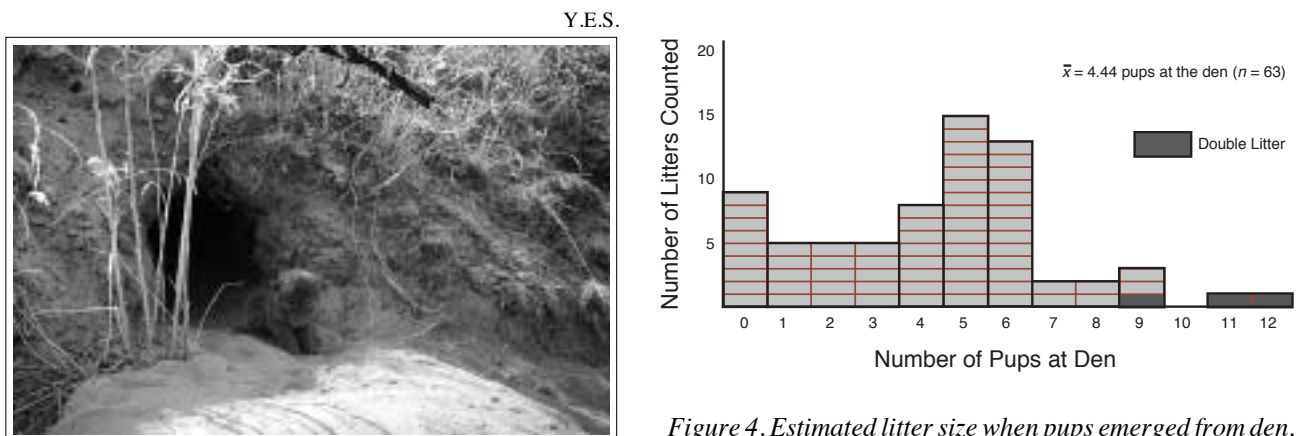


Figure 4. Estimated litter size when pups emerged from den, 1990–1995. Litter size is highly variable on the northern range.

Coyote pups first emerge from dens in mid-May when five-weeks old.

causes of 12 adult mortalities were: mountain lions (4); vehicle (4); and unknown but natural causes (4).

Population Density and Territory Size

Coyotes inhabit all vegetation communities below 8,000' in the GYE except for areas of contiguous deep snow and steep rocky areas. The estimated density of adult coyotes on the northern range averaged 0.45 per km². In the open shrub-steppe and mesic grasslands of the GYE, coyotes can reach densities exceeding 1.0 per km². This estimate is based on both a direct count and an indirect estimate using a method developed by Crabtree (1989) that utilizes the ratio of marked to unmarked scats collected on transects. However, across much of the forested habitat of the GYE, densities range from 0.1 to 0.4 coyotes per km².

The coyote territories we identified on the northern range prior to wolf reintroduction (Fig. 5) were contiguous, non-overlapping areas of 7 to 12 km² (mean = 10.1). Coyotes defended their territories by vocalization, physical presence, and scent-marking (urine and feces). Observations of scent-marking and territorial defense indicated relatively little if any overlap between groups. Territory size and shape are a function of many factors including prey availability, coyote pack size, and the presence of neighboring packs.

The boundaries of territories in the Lamar Valley and Blacktail Plateau areas were extremely stable from 1990 to 1995. Only four boundary shifts occurred over 93 territory-years, and none lasted more than one year. Two of the shifts involved territorial reductions associated with loss of an alpha; the new territorial area still included over 50 percent of the original area. The other two shifts appeared to be associated with access to prime vole habitat when vole numbers were high. Five of seven coyote denning areas found by Robinson and Cummings (1951) on the northern range in 1946–49 were in the same location in 1990–93.

These data, combined with the slow turnover of alpha pairs residing in a territory (average = 6 years) and the consistency of their diet more than 50 years (Table 1), suggest that coyotes invaded

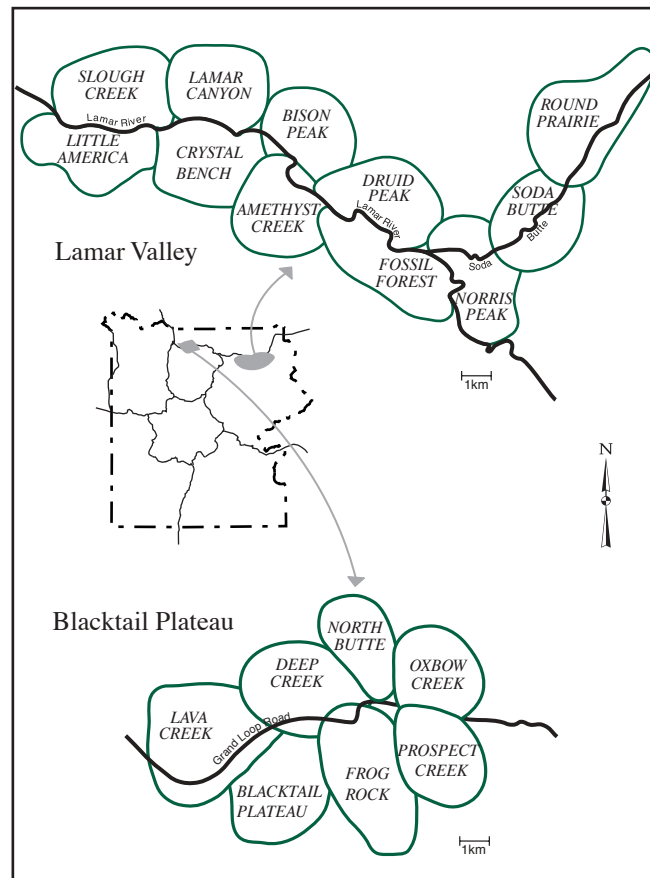


Figure 5. Location of coyote territories in the two study areas on the northern range prior to wolf reintroduction (1990–1995).

suitable habitats vacated by extirpated gray wolves and that the location and number of their territories remained stable until wolves returned in 1995.

Overall dispersal rates in Yellowstone were low compared to other studies. The mean annual dispersal rate was 22 percent for pups and 16 percent for pack members (only subordinate betas dispersed). Movement of radio-tagged juveniles in Yellowstone indicated that some juveniles dispersed in fall or early winter but returned to their natal territories later in the winter or in the spring before whelping. Delayed dispersal may have been the result of habitat saturation—no territorial

vacancies were available for dispersing juveniles.

Food Habits

The two most important coyote food items in our study areas were microtines (voles) and carcasses, mostly elk (Fig. 6). Nearly 50 percent of the coyotes' annual biomass intake came from small mammals. In the seven non-winter months, voles, pocket gophers, ground squirrels, and snowshoe hares made up 41, 25, 3, and 4 percent of prey biomass consumed, respectively, compared to, an estimated 26 percent during the five winter months

Table 1. Coyote food habits.

Prey Species	% of coyote diet Murie 1940	% of coyote diet This study 1995
<i>Microtus</i> spp.	42.4	41.3
Pocket gopher	27.0	24.5
Ground squirrel	0.6	3.0
Snowshoe hare	4.3	4.4
Elk	20.3	21.2

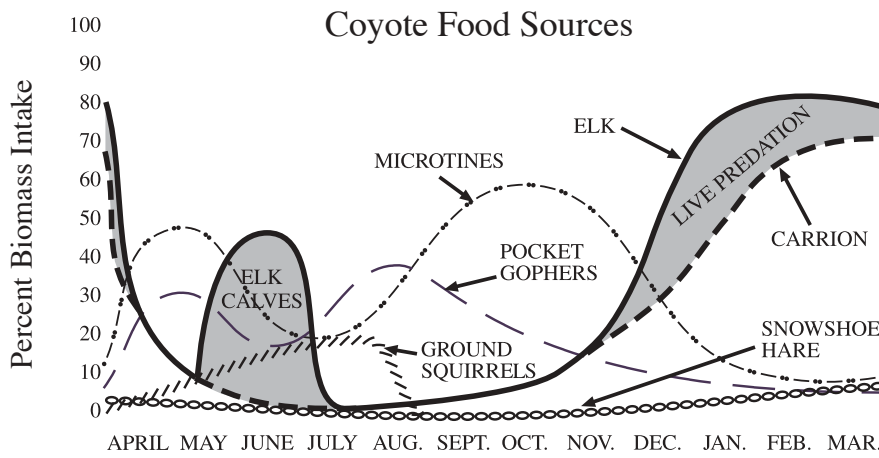


Figure 6. The two most important coyote food sources are microtines (voles) and elk carrion (1990–1995).

from all small mammal prey, mostly voles. Voles were primarily utilized from the early spring snowmelt period until early to mid-winter, after which dense snow prevented coyotes from capturing them (Gese et al. 1996a).

About 45 percent of the coyotes' annual biomass intake came from ungulates. During the five winter months, an estimated 74 percent came from elk, primarily carrion. Carcasses were used only from mid to late winter, except in habitats where coyotes could displace mountain lions from their ungulate kills (Murphy 1998). In the non-winter months, elk (calves and carrion) made up 21 percent of prey biomass consumed.

Prior to wolf reintroduction, coyotes were the major elk predator on the northern range, killing an estimated 1,276 elk annually (Table 2). The coyote population accomplished this not by specialization, but by sheer numbers ($n = 450$). They also exhibited a propensity for kill-

ing, mostly young neonates in June (an estimated 750 annually). A major impetus for this is the availability of prey during May, June, and July when coyote pups are growing rapidly. In Yellowstone, we commonly found elk calf remains at coyote den sites. Coyotes may also inflict heavy predation (>80%) on radio-tagged antelope fawns (D. Scott 1994, pers. commun.).

Coyotes usually kill ungulates that are weak, impaired, domesticated, or starving, but occasionally can kill healthy adult ungulates, even elk. We recorded 26 coyote predation attempts in the Lamar Valley from 1990 to 1995, and detailed observations of nine of these attempts on both adult and younger (<5 months) deer and elk during the winter were reported by Gese and Grothe (1995). Successful attacks were related to deeper snow, and nearly all attacks were led by the alpha male. Two or three adults participated, while the remainder of the pack watched

or was absent (mean pack size was 6.7 adults), yet most pack members fed on both preyed upon and winter-killed ungulates (S. Grothe, unpubl. data).

Although coyotes are capable of killing healthy adult elk during winter, Gese and Grothe found that they seldom do so. In comparison, mountain lions—specialized obligate ungulate predators—kill around 600 elk (and only 35 neonates) on the northern range each year (Murphy 1998). Grizzlies kill an estimated 750 neonates and a few adults (B. Blanchard, pers. commun.).

Ecological Relationships Between Coyotes and Prey Species

Despite major differences in carcass and vole biomass during the 1990–95 period, there was little change in coyote numbers, which varied between 42 and 58 individuals among the seven packs intensively monitored in the Lamar Valley. But individual pack sizes did correspond to prey abundance.

Analysis on a per territory basis in the Lamar Valley revealed vole biomass to be a significant predictor of coyote pack size ($r^2 = 0.34$, $p = 0.035$) and a factor affecting litter size. In wet years, vole biomass is very low in the extensive mesic grasslands due to the effect of flooding on reproducing adults (Johnson and Crabtree 1999). In dry years, vole biomass is relatively high in these dense grass floodplain habitats but low in upland grasslands. Although the relationship between annual litter size and vole populations was marginally significant ($p = 0.07$), packs that had low vole numbers due to flooding had significantly lower litter sizes ($p = 0.02$).

Table 2. Yellowstone ungulate predators.

Species	Estimated Number	Elk Population				Total	Biomass	Per Capita Kill Rate
		Neonate Calves	Yearlings	Adults Winter	Adults Non-Winter			
Mountain Lion (a)	17	35	313	70	193	611	76,150	36
Grizzly Bear (b)	60	750 (b)	0	0	Few	750	13,500	13
Coyote (c)	450	750 (b)	360–626	20–35	0	1,276	66,760	3

- (a) Kerry Murphy, Hornocker Wildlife Institute.
- (b) Francis Singer, Biological Resources Division, USGS.
- (c) This study, projected estimates.

Table 3. Short-term (4 and 5 years after) and predicted long-term (11 to 50 years) effects of the 1988 fires on small mammal prey abundance on the northern range of Yellowstone National Park, Wyoming.

Species	Burned Sagebrush Short-term	Burned Forest Long-term	Short-term	Long-term
Uinta ground squirrel	18x increase	Increase	—	—
No. pocket gopher	4x increase	Increase	2x increase	Increase
<i>Microtus</i> spp.	4x increase	Increase	Slight increase	Unchanged
Red-backed vole	—	—	3x increase	Increase
<i>Sorex</i> spp.	14x increase	Increase	3x increase	Increase
Snowshoe hare	—	—	Decrease	Major increase

Carcass availability was primarily a function of winter severity and had a profound influence on coyote demography. The number of winter-killed elk in a territory was a significant predictor of the pack's litter size the following spring ($p = 0.015$). Furthermore, in severe winters, larger packs took advantage of all the available carrion and had both larger litters and higher pup survival rates (Crabtree and Varley 1999).

As previously stated, the number, size, configuration, and location of territories were relatively constant. In a habitat-saturated area like the northern range, there was little if any room to adjust territory size in relation to the availability and abundance of prey. Rather, adjustments to varying prey abundance came in the form of changes in litter size, pack size, and dispersal within the confines of stationary territories.

We detected no effects of elk seasonal movements on coyote behavior or population demography. Mule deer occurred at such low densities that any changes in their numbers would be undetectable. However, no significant effects of mule deer would be expected because coyotes rarely utilize them as a prey source; their remains were not observed in the examination of over 500 coyote scats.

Fire Impacts on Coyotes

After the 1988 fires, the portion of burned area in the 12 coyote territories examined ranged from 0 to 52 percent, providing a gradient of burn levels with which to study burn effects on coyotes. Demographic factors like pack and litter size were not significantly affected by burn level. However, coyotes may have benefited indirectly from the fires by

having an increased prey base. Several important small mammal prey species (voles and ground squirrels) were more abundant in burned than in unburned habitats during 1992 and 1993 (Table 3). Because the numbers of voles, and possibly ground squirrels, were significantly related to coyote pack size and probably litter size, we can infer that the 1998 fires were advantageous to the coyote population.

Pack Size and Population Regulation

For the years prior to wolf colonization (1990–95), we divided the data on coyote prey abundance into two fairly distinct categories for analysis: years when food was abundant (1991, 1992, and 1994 in the Blacktail Plateau only, where floods did not affect vole numbers), and years

when food levels were low (1990, 1993, 1994 in the Lamar Valley due to floods, and 1995). In good food years, carrying capacity within the coyote territory exceeded pack size and the number of adult pack members contributed directly to litter size and pup survival. However, because virtually all food consumed by a pack came from within its territory, in low food years the packs may have exceeded territorial carrying capacity, and pack size was negatively correlated with both litter size and pup survival.

The evolution of packs, or sociality, has been attributed to the increased foraging efficiency made possible by pack membership, but this relationship remains unclear. We found no empirical evidence that larger coyote groups have a larger per capita food intake, thus improving fitness. In fact, single individuals and

Jennifer Sheldon



The Druid coyote pack feeds on an elk carcass. Alpha female 620 (left) was killed by the Druid wolves on November 25, 1999.



Druid female wolf 42 chases Little America alpha female coyote 440. She escaped after being bitten.

groups of two coyotes commonly killed both deer and elk in Yellowstone (Gese and Grothe 1995), and dominant coyotes tended to monopolize feeding time on both preyed-upon and winter-killed ungulate carcasses (Gese et al. 1996b). Defense of the carcass appeared to be primarily the role of the dominant alpha male.

Coyote populations are regulated by factors other than prey abundance: territoriality, dominance hierarchy (exclusive breeding by the alpha pair), shortened breeding tenure, subordinate dispersal, delayed dispersal, reproductive failure, double-littering, and early and late summer pup mortality. Most studies indicate direct or indirect evidence of intraspecific competition, especially in unexploited and habitat-saturated populations, as evidenced by low pup weights, scarring, reproductive failure, frequent territorial disputes, and high pup mortality, including the probable loss of entire litters shortly after birth. The abundance and availability of prey is certainly a major limiting factor, but the extent to which it is involved in population regulation remains uncertain.

The Return of Wolves: Changing the Coyotes' World?

Prior to wolf restoration, between 85 and 90 percent of the northern range coyote population existed in packs and

average pack size was high. The extirpation of gray wolves probably permitted higher coyote population densities, and coyotes at least partially slid into the niche left vacant. This could account for two key findings of this study: coyotes were a major elk predator, and they consumed a very high percentage of the available small mammal prey, probably to the detriment of other small mammal predators.

Since the restoration of gray wolves in 1995, the ecological role of the coyote has already shifted numerically, functionally, and behaviorally. The gray wolf is a much larger animal—the average adult weight of the males brought from Canada was 111 pounds, and for the females, 94 pounds, while adult coyotes examined on the northern range have weighed an average of about 30 pounds for males and 26 pounds for females. So far, gray wolves have inflicted heavy mortality on coyotes (Crabtree and Sheldon 1996), killing from 25 to 33 percent of the coyote population each winter, especially in the wolves' core-use areas. In over 200 coyote-wolf interactions observed since 1995, we have witnessed wolves killing coyotes 23 times. The sex and age structure of both these coyotes and others that were probably killed by wolves, suggests that wolf killing is opportunistic, with a possible bias toward younger coyotes. Of the 34 coyote

carcasses we recovered, 20 were fairly intact (scavengers hadn't yet fed on them) and close examination revealed that the deaths had been caused by severe bites to the chest area resulting in broken ribs and internal bleeding. All but one death occurred in relation to scavenging behavior at wolf-killed elk carcasses.

When the wolves were released in 1995, the Lamar Valley was populated by 80 coyotes in 12 packs with an average pack size of 6; by 1998, the count had dropped to 36 coyotes in 9 packs with an average pack size of 3.8. Based on this data, it appears that the killing of coyotes by wolves during the winters of 1996–97 and 1997–98 resulted in a 50 percent reduction in coyote numbers and significantly reduced pack size on the northern range, without subsequent recolonization of traditional coyote territories. Coyote packs in this core area of wolf territories either disappeared or were in a constant state of social and spatial chaos. In 1998, only one pack of three coyotes and a handful of transients occupied the core area of the Druid wolf pack, along lower Soda Butte Creek where it joins the Lamar River. Before wolves, there had been four packs totaling about 30 coyotes.

But there seems to be safety in numbers. Prior to wolf restoration, coyotes normally traveled singly or occasionally in groups of two or three; now they are now much more cohesive and tend to travel with most of their pack—we have observed traveling groups as large as nine. Packs on the fringe of wolf territories, which are fairing better, number from six to ten individuals and have experienced little mortality, yet they are close enough to effectively scavenge wolf kills.

When coyotes outnumber a single wolf or pair of wolves, the tables can turn. Coyotes have chased and even attacked individual wolves and wolf pups. When a pack of three or more coyotes encounter a single wolf feeding on kill, the coyotes may occasionally harass the wolf and chase it off. When coyote and wolf groups of similar size (3 to 6 animals) encounter each other, they may watch each other closely and sometimes engage in a battle. Occasionally groups of wolves will chase groups of coyotes; we have witnessed a lot of growling and occasional nipping, but no serious contact or death.

At least six coyote dens were partially excavated by wolves, and the coyotes responded by denning in or under large rocks and moving their dens away from areas frequented by wolves. Placing dens farther from preferred foraging areas could increase the effort required of adult pack members to feed the pups. However, this negative effect is being offset; some of the surviving coyote packs are smaller in size and are producing, on average, heavier pups with higher survival rates.

These changes could have major ripple effects on both the coyotes' competitors and their prey species. Fighting, killing, chasing, and relegation to inferior habitats has been clearly demonstrated between coyotes and wolves (Crabtree and Sheldon, in press). Yet wolves, coyotes, and even red foxes continue to coexist in the Northern Rockies. We believe that the coyote's behavioral plasticity and demographic resiliency to exploitation is an evolutionary product of coexisting with competing species, mainly the gray wolf. Since wolves have returned to Yellowstone, coyote populations have become wiser and more wary. They certainly will survive, and will very likely continue to outnumber wolves. We believe that conservation science can learn important lessons from long-term studies of a successful, ubiquitous species like the coyote in unexploited populations such as exist on Yellowstone's northern range. We hope to continue our studies post-wolf to provide such understanding.

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References

- Crabtree, R. L. 1989. Sociodemographic characteristics of an unexploited coyote population. University of Idaho, Moscow.
- Crabtree, R. L., F. G. Burton, T. R. Garland, D. A. Cataldo, and W. H. Rickard. 1989. Slow-release radioisotope implants as individual markers for carnivores. *J. Wildl. Manage.* 53:949-954.
- Crabtree, R. L. and J. W. Sheldon. 1996. Summary of the interactions of gray wolves and coyotes on Yellowstone's northern range. Special Report to Yellowstone National Park.
- Crabtree, R. L. and J. W. Sheldon. In press. Coyotes and canid coexistence in Yellowstone. In T. Clark, P. Curlee, P. Kareiva, and S. Minta, eds., *Carnivores in Ecosystems: The Yellowstone Experience*. Yale Univ. Press, New Haven, Conn.
- Gese, E. M. and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *Am. Midl. Nat.* 133(1):36-43.
- Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996a. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. *Can. J. Zool.* 74:784-797.
- _____. 1996b. Social and nutritional factors influencing the dispersal of resident coyotes. *Anim. Behav.* 52:1025-1043
- Hatier, K. G. 1995. Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming. Montana State University, Bozeman, Mont.
- Johnson, K. A. and R. L. Crabtree. In press. Small prey of carnivores in the greater Yellowstone ecosystem. In T. Clark, P. Curlee, P. Kareiva, and S. Minta, eds., *Carnivores in Ecosystems: The Yellowstone Experience*, Yale Univ. Press, New Haven, Conn.
- Moorcroft, P. R., M. A. Lewis, and R. L. Crabtree. 1999. Home range analysis using a mechanistic home range model. *Ecology*: 80:177-186.
- Murie, A. 1940. Ecology of the coyote in the Yellowstone. U. S. Nat. Park Serv. Fauna Ser. No. 4. U.S. Govt. Printing Office, Washington, D.C.
- Murphy, K. M. 1998. The ecology of the cougar, *Puma concolor*, in the northern Yellowstone ecosystem: Interactions with prey, bears, and humans. Ph.D. diss., Univ. of Idaho, Moscow.
- Robinson, W. B., and M. W. Cummings. 1951. Movements of coyotes from and to Yellowstone National Park. U.S. Fish and Wildlife Service special scientific report on wildlife No. 11. USDI Fish and Wildlife Serv., Washington, D.C.
- Schullery, P., and L. Whittlesey. 1992. The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882. Pages 1-3 to 1-174 in J. D. Varley and W. G. Brewster, eds., *Wolves for Yellowstone? A report to the United States Congress*, vol. 4, research and analysis. National Park Serv., Yellowstone National Park.
- Sheldon, J. W. 1992. *Wild Dogs: The natural history of the nondomestic Canidae*. Academic Press, San Diego, Calif.

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