ABSTRACT

Sixty-five healthy coyote (Canis latrans) adults and 53, 8-12 week old pups captured at dens were radio-tagged in the Lamar Valley and Blacktail Plateau areas of the northern range of Yellowstone National Park. Adults range in age from 1 to 11 years and averaged nearly 3 years old. Territorial packs in both study areas are adjacent, non-overlapping, contiguous, and averaged 15 km². Based on information the last three winters and data collected from 1946 to 1949, territorial areas are traditional and have changed little in the last 45 years. We estimate that 85 to 90% of coyotes on the northern range belong to packs. A territorial group or pack during the winter consists of 2 alpha individuals, 2 or 3 beta adults, and 2 or 3 adult-sized pups (average pack size = 7). Only one radioed adult coyote has died since May of 1992. Twenty-four of 53 pups have died between the ages of 3 and 9 months old. Population productivity ranges from 1.8 to 2.5 pups recruited per territory. The reproductive failure rate among breeding groups averaged 15% during 1990 and 1991. Initial density estimates are 1.4 coyotes per square mile. Intensive foraging observations were conducted from January through June 1991 (353 hours) and from November 1991 through April 1992 (1100+ hours). Focal observations collected from January-June 1991 resulted in 427 capture attempts on small mammal prey with 162 (38%) successful. Habitat type played a key role in the success rate. Preliminary analysis of the November 1991 to April 1992 data indicated a substantial reduction in prey attempts and prey success. This reduction was mostly a function of harsh snow conditions in early winter and abundant elk carrion in late winter. Over eighty ungulate carcass were located this winter in the 2 study areas. However, small mammals, especially voles, dominate the diet with ungulate remains becoming important in May through July (presumably elk calves) and late winter (mostly scavenging).

We have documented numerous successful and unsuccessful predation attempts on ungulates in our study areas. Coyotes appear to impact ungulate numbers in 3 ways: predation on calves and fawns shortly after birth (up to 8 weeks), predation on short-yearlings and adults during winter, and indirect impact from harassment of other predators at ungulate-kills. Coyotes may be the major ungulate predator on the northern range due to cooperative social and foraging behavior, their ability to take advantage of vulnerable ungulates, and their high population levels. Wolf extirpation has probably resulted in high coyote population densities and coyotes have, at least, partially slid into this vacant niche.

INTRODUCTION

The ecology of natural, unexploited coyote populations is, for the most part, unknown. Whether research is management-oriented or of evolutionary significance, the ecology of natural coyote populations must be understood in the absence of human exploitation. Yellowstone National Park should provide the ideal situation for such an
investigation. Not since Adolph Murie's landmark study 50 years ago (Murie 1940) has a comprehensive, objective study of coyote ecology been undertaken in the Yellowstone ecosystem.

The objectives of this project are to:

1. Assess effects of 1988 fires on coyote survival, reproduction, activities, pack and territorial dynamics.

2. Estimate coyote population density and quantify their ecological role preceding potential wolf (Canis lupus) restoration.

3. Quantify the effect of winter elk carrion availability and mule deer (Odocoileus hemionus) density on coyote population dynamics.

4. Describe coyote seasonal responses to movements of elk (Cervus elaphus) and mule deer.

5. Test if coyote pack size is related to prey size, territory size, size of litters, and pup survival.

6. Describe interspecific interactions among scavengers.

7. Document predation of coyotes on ranch livestock by coyotes from Yellowstone, and on allotments on National Forests adjacent to the northern range.

8. Develop and test a social-class structured population model in comparison to sex-and age-structured approaches.

9. Estimate parameters for, and develop an empirically-based energetic model that explains the variation in spatial location, movement, and reproductive success of coyotes based on various underlying themes (prey base, habitat, slope, aspect, etc.).

Kezha Hatier began collecting data on how beta pack members on the Northern Range influence pup survival via feeding and den guarding. Scott Grothe will begin collecting data this winter on carcass use and how carrion availability affects social and population parameters of coyote packs. Their work is part of their Masters and Ph.D. research, respectively, at Montana State University. For specific methodology see Crabtree (1991).

♦ RESULTS AND DISCUSSION

Field work began in fall 1989 in the Lamar Valley and Blacktail Plateau areas of northern Yellowstone. Since then we have maintained our goal of 1 to 3 marked adults in all social groups in both study areas. Lamar Valley has 7 social groups or "packs", whereas Blacktail Plateau has 6. Including only the areas adjacent to, and either side of the paved highway there are 21 social groups from the west end of Blacktail Plateau to the east end of Lamar Valley.

Sixty-five adult coyotes have been captured (27 F, 28 M) in Lamar and Blacktail areas during fall/winter and spring trapping periods. Fourteen coyotes were trapped and radio-collared in fall 1992 (10 adults and 4 pups), which included 3 recaptures. Seven of these were instrumented with activity collars. Trap success was high and still averaged approximately 42 trap nights/coyote. Four badgers (Taxidea taxus) were also captured this fall. The age of trapped coyote adults (11+ months and older) ranged from 1 to 5 yrs and averaged 3.3 yrs. To our knowledge this is the oldest average age yet reported in any coyote study.

Twenty-seven pups were hand-captured at dens in June 1992. Pups were isolated from den entrances and "grabbed" or were forced out of their dens with a wire-ferret device. Twenty-one of these were surgically implanted with a intraperitoneal transmitter (45 g) and released. Six pups were not implanted because of their low weight and poor condition.

SOCIAL AND SPATIAL ORGANIZATION

Territorial packs in both study area are adjacent, non-overlapping, contiguous, and averaged
Evidence strongly indicates that coyote territories are traditional and have not shifted spatially in over 45 years. The location of dens discovered in 1946 to 1948 were compared to the location of dens discovered in 1990 to 1992. Five of 7 den areas were still being used. In addition, the boundary regions of 8 territories have not changed from winter 1989-90 to winter 1991-92.

We estimate that 85 to 90% of coyotes on the northern range belong to packs. As in other studies of coyote social ecology, a northern range pack or territorial group consists of a dominant, mated alpha-pair and subordinate "beta" individuals. These betas are pups from previous litters that remain in the natal area.

We calculate that during the winter an average northern range pack consists of 2 alpha individuals, 2 or 3 beta adults, and 1 to 3 adult-sized pups (average pack size = 7). Approximately one beta adult in each pack has a loose affiliation with its natal area and has a movement area much larger than the territory size. The average pack size during winter 1991-92 was 6.5 compared to 7.1 the previous winter.

Preliminary results of carcass observations suggest that pack access to a carcass is a function of initial discovery, its location with respect to territorial boundaries, and level of hunger. Within a pack, the alpha male has first feeding access and is occasionally tolerant of the alpha female but not subordinate betas and pups.

POPULATION DEMOGRAPHICS

Based on visual capture-recapture and territory enumeration the population density of coyotes on the northern range appears to be very high. Preliminary estimates averaged 1.4 adult coyotes per mi². Density appears stable and we have detected no significant changes over 3 consecutive winters. We are currently finishing the counting of scats for presence of the isotope-label. Over twenty percent of the first 850 scats counted were labeled. This ratio of marked to unmarked scats will allow an independent estimate of population density.

Although some coyotes have dispersed from their natal pack territories, we are aware of only one adult mortality since May of this year. A radio collared female from the Lava Creek pack was shot by hunters on Deckered Flats near Gardiner.

Disease took its toll on pups on the northern range this past summer. Necropsies determined that six of the 10 implanted pups, and one non-implanted pup in the Blacktail study site died from parvovirus. Two others died of unknown causes. However, only one of 11 implanted pups in Lamar Valley was found to have died from parvovirus. Mortality rate of pups implanted this past summer was 43%.

FORAGING ECOLOGY

Eric Gese, University of Wisconsin-Madison, observed 17 coyotes (10 M, 7 F) from 15 January to 15 April 1991. A total of 223 hours of observation were collected on foraging and social behavior (including mating and scent-marking behavior). We observed 264 capture attempts with 92 (35%) successful. Habitat type played a key role in the success rate. Mesic meadow and mesic shrub/meadow habitats had the highest capture rate at 36% and 44%, respectively. Sage habitat had the lowest success rate at 28%. These different success likely reflected different prey densities and prey vulnerabilities.

Thirteen coyotes (10 M, 3 F) were observed from 16 April to 15 July 1991. A total of 130 hours of observation were collected on foraging and social behavior including adult-pup interactions and territorial defense. We observed 163 capture attempts with 70 (43%) successful. Mesic meadow and mesic shrub/meadow habitat, again, had the highest success rate at 47% and 40%, respectively, whereas sage habitat was low at 33%. Further analysis of foraging rates will include the influence of snow depth and type, habitat, sex, social class, age, and weather.

Over 1100 hours of foraging observations were collected from November 1991 through April 1992. Preliminary analysis of the November 1991 to April 1992 data indicated a substantial reduction in prey attempts. This reduction was mostly a function of harsh snow conditions in early winter and abundant elk carrion in late winter. Over 100 ungulate carcass were located this winter in the 2 study areas.

The 170-mile scat-survey transects conducted...
at the end of each biological season results in the collection of 300 to 400 samples. We have subsampled 160 scats from each collection period and have begun analysis of food habits and estimates of prey biomass consumed. Preliminary results indicate that small mammals, especially voles, dominate the diet with ungulate remains becoming important in May through July (presumably elk calves) and late winter (mostly scavenging).

We documented numerous successful and unsuccessful predation attempts on ungulates in our study areas. Coyotes appear to impact ungulate numbers in 3 ways: predation on calves and fawns shortly after birth (up to 8 weeks), predation on short-yearlings and adults during winter, and indirect impact from harassment of other predators at ungulate-kills. Although coyote predation on ungulates has not been directly looked at, the following information strongly suggests that coyote predation on ungulates is a significant factor and that the coyote is currently the major ungulate predator on the northern range. Of course this could dramatically change with the recolonization of wolves.

A recent elk calf mortality study (B. Harting, unpubl. data 1991) indicated a 7, 7, 10, and 35% annual coyote predation rate in Lamar Valley during 1987, 1988, 1989, and 1990, respectively. This corresponds to the remains of 1 to 3 elk calves per coyote den found during June at both study areas in 1990 and 1991. Based on searches of denning sites (coyotes generally move 4 or 5 times the first 10 weeks after birth) we calculate a minimum of 8 calves killed (and brought back to the den) per territorial pack. We also have found intact elk calves killed by coyotes and not utilized.

Based on preliminary analysis of a small sample of marked pronghorn fawns and fawn/doe ratios, it appears that coyote predation was 80% on northern range pronghorn fawns in 1991 (D. Scott, pers. commun. 1991). We also suspect high coyote predation rates on mule deer fawns.

Coyote predation on elk during the winter months appears to be a function of increased vulnerability: snow conditions and slope (G. Green, pers. commun. 1988) and the size and condition of short-yearlings. Besides noting several successful and unsuccessful predation attempts on short-yearling elk (and one successful attempt on an adult mule deer), we noted a healthy 2 or 3 yr. old cow that was attacked and killed by a pack of coyotes in Lamar Valley in February 1990. During carcass surveys conducted on the northern range in 1987 researchers were able to verify that coyotes killed 3 of 5 short-yearling elk for carcasses discovered 0 to 4 days after death; and 2 of 7 short-yearlings 4 to 16 days after death. An additional 28 short-yearlings were found 16 to 90 days after death but cause of mortality could not be attributed to a predator.

Another means by which coyotes numerically impact ungulate populations is through harassment of other ungulate predators thereby forcing them to abandon their kill and kill ungulates at a higher rate. During intensive observations in recent years coyotes have been observed usurping both mountain lions and grizzly bears from their kills. Without coyote harassment lions apparently spend 2 to 3 times longer feeding at a kill (G. Felzien, unpubl. data 1991). In one instance, a coyote pack was observed usurping, attacking, and biting a grizzly bear (S. French, pers. commun. 1991).

Although it is difficult to quantify the direct impact of coyotes on ungulate populations it is feasible that coyotes could be removing 1000 or more elk annually. The average percent elk calf mortality reported above was 15%. Crudely extrapolated to the northern range, fifteen percent of, say, 6000 elk calves in 900 elk removed by elk calf predation alone. Compared to an estimated 350 to 400 elk removed by mountain lions annually (K. Murphy, pers. commun. 1991) coyotes may present a significant influence on ungulate populations (especially on low populations of pronghorn and mule deer). This impact is function of coyote population size which may be at unnaturally high levels due to the extirpation of wolves. Based on extrapolations from our study areas to other similar areas on the northern range with known coyote presence we estimate at least 450 coyotes (60 packs) on the northern range.

♦ CONCLUSIONS

The northern Yellowstone population has characteristics similar to the natural, unexploited population in south-central Washington studied by Crabtree (1989): low productivity, a highly-structured social system, a contiguous distribution of non-
overlapping, year-round territories, and an old-age structure. Adult mortality is low and primarily due to mountain lions. Like gray wolves (*Canis lupus*), 85 to 90% of northern Yellowstone coyote population exists in packs and average pack size is high. Northern range coyotes prey primarily on small mammal prey, but ungulate prey is a significant food source seasonally. Coyotes may be the major ungulate predator on the northern range due to cooperative foraging behavior, their ability to take advantage of vulnerable ungulates, and their high population levels. Wolf extirpation has probably resulted in high coyote population densities and coyotes have, at least, partially slid into this vacant niche.

**LITERATURE CITED**

