Effects of 1988 Fires on Ecology of Coyotes in Yellowstone National Park: Baseline Preceding Possible Wolf Recovery

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◆ **Abstract**

Sixty healthy adult coyote *Canis latrans* 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 12 years and average nearly 3.3 years old. Territorial packs in both study areas are adjacent, non-overlapping, contiguous, and average 15 km^2. Based on information from the last four 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). Fifteen marked coyotes have died since November of 1992. Initial density estimates are 1.4 coyotes per square mile. Preliminary scat analysis suggests 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).

Two graduate students have finished their data collection and another student is currently working on his last field season. More than 2500 hours of foraging observations were conducted from January 1991 through June 1993 resulting in data collection on more than 4400 predation attempts on small mammals. Eight hundred and fifty hours of den observations were completed during 1992 and 1993. Beta pack members were observed to bring food to pups and protect den sites from intruders. Coyote behavior and ungulate mortality data were collected on sixty-one carcasses found during the 1992-1993 winter.

Five successful and 4 unsuccessful predations by coyotes on ungulates have been seen. 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 their cooperative social and foraging behavior, ability to take advantage of vulnerable ungulates, and 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.

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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.).

Eric Gese has finished his data collection in the field and is currently analyzing data and taking courses toward his doctorate at the University of Wisconsin (Madison). He expects to complete his degree requirements by the end of 1994. Kezha Hatier has also finished collecting data on how beta pack members on the Northern Range influence pup survival via feeding and den guarding. She is taking courses toward her Master's degree at Montana State University and expects to fulfill her degree requirements by the end of 1994. Scott Grothe is mid-way into his last field season of data collection to examine how carcass use and carrion availability affects social and population parameters of coyote packs. He is working on his Ph.D. at Montana State University and expects to complete his degree requirements by the end of 1995.

♦ METHODS

GENERAL POPULATION DEMOGRAPHY AND SOCIAL ECOLOGY

In the present and ongoing studies, adult coyotes are captured with padded, offset leg-hold traps (Soft-catch, Woodstream, Inc.) with attached tranquilizer tabs (Balser 1965) and other injury-minimizing (and avoidance of non-target species) modifications developed by Crabtree (1989) who incurred no major injuries and no deaths in 121 captures of 112 individual coyotes. We also capture coyotes with a remote-triggered, fence-net near carcasses during winter.

The sex, weight, estimated age, condition indices (Crabtree 1989), presence of scars and unique marks, and description of genitalia and mammae are determined for each coyote. The vestigial first premolar is extracted from an anaesthetized lower jaw for age analysis via cementum annuli examination. Each coyote is ear-marked and fitted with a modified (Crabtree 1989) 3-year radio collar weighing 3% of body weight. Blood samples will be taken in future studies for serological analysis and DNA fingerprinting.

All baseline ecological data is collected according to 3 biological seasons: **whelping**, 15 April to 15 July; **pup-rearing**, 15 July through 15 October; and **winter** (breeding), 15 October through 15 April. At the end of each biological season pre-defined transects are canvassed to collect coyote feces. This allows correlation of biological-season specific movements, habitat use, and behavior with foraging ecology and food habits.

Coyotes in ongoing studies will be radio-tracked with a variety of techniques including a fixed-station null-peak system. Resident coyotes will be

located every hour during 12 night sessions each biological season. Coyotes will be located only during active periods determined by remote activity-monitors and infrequent 24-hour sessions. Non-resident coyotes will be monitored approximately two times per week. Individual resident coyotes will be monitored approximately two times per week. Individual residency times (Crabtree 1989) on the pre-selected core study area will be estimated to aid in the determination of social class, population social composition, and population density (Dennis et al. 1991). Coyotes will be assigned social status based on the classification criteria of Crabtree (1989) who studied a natural, unexploited population.

The above methods will allow for the estimation of emigration (dispersal), immigration, survival, mortality factors, territorial turnover, social class transition probabilities, and population productivity. Maximum-likelihood estimates of survival and mortality factors will be generated with program SURVIV (White 1984) and modified with the Kaplan-Meier staggered-entry models (Pollock 1989). This analysis will allow survival and mortality factors to be estimated and statistically tested by year, age class, social class, season, and sex. Litter size will be determined from den counts and occasional (if any) female carcasses. The proportion of females in the population that breed will be estimated from activity and movement data during whelping as verified by Crabtree (1989). A modified Markov transition/Leslie matrix model based on social-class specific mortality and fecundity will be constructed (Crabtree, unpublished manuscript) to estimate population growth rate and social-class transition probabilities.

In future studies, pups will be hand captured at dens when 9-12 weeks old and surgically implanted with intraperitoneal radio-transmitters. This will allow estimates of early pup mortality, dispersal, and social interaction and transitions up to 2 years of age.

Coyote home ranges and utilization distributions (probability density functions) will be estimated with an adaptive kernel method (Worton 1989) using a recently developed computer program (see Chow and Crabtree 1989). For comparative purposes the minimum convex polygon (Mohr 1947) and harmonic mean (Dixon and Chapman 1980) methods will be calculated. Seasonal spatial overlap indices will be calculated based on volume overlap of animals' utilization distributions (program OVERLAP

[Leban and Crabtree 1988]).

SPECIFIC METHODS FOR FIELD-ORIENTED OBJECTIVES 1 THROUGH 7

1. We will quantify the following coyote responses: survival, reproduction, changes in social status, territoriality, group size, food habits, prey consumption, seasonal home range shifts, and foraging activity and location. We will treat the territory or coyote social group as the sampling unit and conduct a "gradient analysis" (Ter Braak and Prentice 1988) in the form of a linear model. Extensive effort will be placed in capturing at least one or both) alpha adult(s) in at least 12 territories located across a gradient of fire intensities and burn types (e.g., forest, shrubland, and sedge) with 4 of 12 territories located in unburned, "control" areas. We simply seek to explain the variation among territorial group response variables (dependent variables above) by measurement of habitat variables such as cover, burn characteristics, and prey abundances of each territory (independent variables).

2. We will utilize a modified mark-recapture method known as radioisotope feces-tagging that has much promise and has recently been implemented to directly estimate coyote population size and density (Crabtree et al. 1989, Dennis et al. 1991). Captured coyotes are administered a tag that marks the feces. This averts recapture biases, eliminates the need for recapture of coyotes, and provides large sample sizes and more precise estimates.

We propose 2 unique and innovative approaches to determine the ecological role of the coyote with emphasis on their impact on prey species. First, we will utilize a differential digestibility model recently developed and apply it to our population of coyotes. Secondly, we will estimate predation rates on prey species based on the highly observable and habituated coyote population of Yellowstone's northern range.

We will not only examine food habits from scat analysis but apply a method that estimates the actual fresh weight of prey ingested for each prey species (elk, mule deer, antelope, microtines, pocket gophers, etc.). This differential digestibility model was recently completed (Kelly 1991). This model corrects the bias due to differential digestion of prey items. This research was the result of an extensive,

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highly controlled and replicated series of feeding trials involving 50 coyotes, 37 prey species combinations, and multiple examination of over 1,600 coyote scats. Differential digestibility of different prey types caused a severe bias which means current methods are highly inaccurate. Even the gross ranking of preferred food items based on percent frequency of occurrence of prey items in scats can be highly misleading. Differential digestibility was found to be a complex function of physiological parameters such as feeding time strategies, retention time and passage rates in the stomach, and surface area to volume ratios of prey types.

Besides the application of the differential-digestibility model, the key to estimating the actual biomass of prey consumed by a population of coyotes (e.g., Lamar Valley) is estimating the population size of coyotes (this we have completed) and estimating coyote defecation rates. There are 3 ways we propose to obtain estimates of the unknown, but critically important estimate of defecation rates. First, the above pen study will provide an estimate, but a degree of uncertainty exists as to whether this is representative of the real field situation. A second estimate can be obtained from dividing the total number of observed defecation by the total number of observed coyotes-hours. A third estimate can be obtained from snow-tracking coyotes and recording the distance in between defecation. Because the routes of snow-tracked coyotes can be determined from radio-tracking, the distances between defecation can be converted into time-specific rates. Other events revealed from snow-tracking like urination scent-marking and predation attempts can similarly be converted to time-specific rates.

Because we can collect a sample of scats from the interior core area of a territory with certainty that those scats are from that pack we can again, determine the effect of fire, available prey, group size, etc. on prey type consumed. Crabtree et al. (1989) individually marked and identified the scats from 44 coyotes and verified that over 95% of the scats collected from inside the home-range core area are from the resident pack themselves.

3. We will estimate both the availability of elk carrion (and other ungulate carrion) and mule deer density and relate this to coyote population dynamics at 2 levels: the individual territory and the total coyote population (over time). Concurrent with the winter transects addressed in objective #6, we will conduct winter ground transects on the northern winter range in order to estimate the availability of carrion. Estimates of mule deer density will be gathered from other ongoing research efforts in the park.

Thus, as in objective #1, an individual territorial group's survival, reproduction, change in social status, territoriality, group size, food habits, prey consumption, seasonal home range shifts, and foraging activity and location will be related to, and tested for the availability estimates of carrion and mule deer (gradient analysis). Additional estimates of other ungulate prey (e.g., antelope fawns) may also be addressed in the same manner as mule deer availability.

4. We will examine the following coyote responses to ungulate movements both to and from the winter range at both the territory and population level: diet shifts, changes in activity patterns, territorial behavior and carcass interactions (objective #6), home range shifts, and pack size. The radio-telemetry and winter observational data will be analyzed temporally with divisions centered on spring and fall ungulate migrations, coyote breeding and pair bonding, and alpha female parturition and weaning periods. Finally, paired comparison of responses will be made between territorial and non-territorial individuals.

5. Group or pack size will be determined by a combination of methods: visual sightings from ground and aerial observation during December through March when group cohesiveness is maximized, ratio estimate from marked feces (Crabtree et al. 1989), and most importantly vocalization monitoring and carcass observations.

6. Besides the nocturnal and crepuscular radio-tracking periods during the winter period we will conduct a supplemental study. We will observe coyote interactions at carcasses utilizing modified focal sampling procedures (Altmann 1974) and record behavioral information into a palm-top computer, cassette tape, and/or video recorder. Behavioral interactions such as dominance display, fighting, and usurping within and between coyote packs will be recorded in relation to these various factors: territorial area (core area, periphery, and boundary), group size, carrion availability, season, sex, food deprivation/satiation, and age of territorial establishment. Supplementation of carcasses to

improve a balanced design and create carcass interactions at observational vantage points will be conducted.

Concurrent with carcass transects (objective #3) we will record all predator tracks (coyote, red fox *Vulpes vulpes*, bobcat *Felis rufus*, marten *Martes americana*, cougar *Felis concolor*, wolverine *Gulo gulo*, etc.). Besides snow-track surveys, sightings, scats, and possible captures will be monitored to provide a baseline index to abundance before possible wolf presence.

7. There exists no valid method to ascertain actual coyote depredations unless the carcass is fresh. However, we propose to make contact by letter, telephone, and personal visitation to local private ranches with livestock on private and National Forest land. Estimated dispersal rate and dispersal direction from Yellowstone coyotes will be compared on a seasonal and yearly basis to the response by livestock owners and other involved personnel (e.g., Montana Dept. of fish and Game).

From late November 1992 to mid April 1993, 24 hour activity was sampled for coyotes in both study areas with radiotelemetry techniques. A sub sample of daytime telemetry activity estimates were also post-corrected and checked with simultaneous visual observations. These data included date, time, weather conditions (i.e. cloud cover, wind, and temperature), snow cover, sex, age, social status, and pack affiliation for each coyote, and whether the coyote was active or inactive, along with a quality rating of each telemetry reading.

◆ RESULTS AND DISCUSSION

Field work began in fall 1989 in the Lamar Valley and Blacktail Plateau areas of northern Yellowstone. 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.

SOCIAL AND SPATIAL ORGANIZATION

Territorial packs in both study area are adjacent, non-overlapping, contiguous, and averaged 15 km². Evidence from the last four winters 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 1992-93.

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 the 1992-93 winter was 6.2, compared to 6.5 in the winter of 1991-92 and 7.1 in 1990-91.

POPULATION DEMOGRAPHICS

The population density of coyotes on the northern range appears to be high, based on visual capture-recapture and territory enumeration. Preliminary estimates averaged 1.4 adult coyotes per mi². Density appears stable and we have detected no significant changes over 4 consecutive winters. We are currently finishing the scat counts 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.

A total of 113 coyotes were captured and blood sampled from October 1989 to February 1994. Sixty-two males and 51 females were sampled from 16 different resident packs. Age classes of the captured coyotes were 35 adults, 12 yearlings, 13 old pups (5-6 months old), and 53 (8-12 week old) pups. Fourteen coyotes were sampled in 1989, 14 in 1990, 36 in 1991, 38 in 1992, 10 in 1993, and 1 in 1994. Adults ranged in age from 1 to 12 years and average 3.3 years.

Fifteen radio-collared or implanted coyotes were found or presumed dead since November 1992.

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Two were hit by vehicles in the Yellowstone National Park, six died of unknown causes, one was trapped, one was shot, two were recaptured and euthanized for rabies testing, and three collars were returned and these coyotes were presumed dead of unknown causes. One of the latter collars was that of the 13 year old alpha female of the Bison Peak Pack in Lamar Valley. Based on field observations, it is believed that most of the coyotes in the Lamar Valley at this time are descendants of this coyote.

FORAGING ECOLOGY

Eric Gese completed his field work on 1 July 1993. He has returned to Wisconsin to compile and analyze data, prepare his dissertation and manuscripts for publication, and finish his course work. He and field assistants collected in excess of 2500 hours of coyote behavioral and foraging observations on more than 50 coyotes from 5 packs in Lamar Valley. These data include more than 4400 predation attempts on small mammals.

The 170-mile scat-survey transects conducted at the end of each biological season resulted in the collection of 300 to 400 samples per survey. 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 (Gese and Grothe, 1994), 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.

An 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.

Five successful predations of coyotes on adult and short yearling elk calves have been seen as well as 5 unsuccessful attempts (Gese and Grothe, 1994). For these predation events, attacking coyotes used terrain and deep snow to their advantage. Observed attacks usually occurred either in deep snow (> 0.5 m) and/or on a steep slope during both day and nighttime hours. The kills were made by the alpha pair, with the male being the most aggressive. Coyotes would typically bite and hold onto the hamstring of a rear leg to bring down the elk. Usually after an elk was brought down (but, still alive), the alpha pair began feeding, often on the rump and side. However, biting at the head and neck region did occur.

Most of the observed predation attempts that were unsuccessful were attempts on elk calves (Gese and Grothe, 1994). During their escape, calves made their way to bare ground or unfrozen creeks. Calves that got to bare ground had a much better advantage at warding off an attack with head butts, kicks, and quick turns. Coyotes would not follow calves into open water, but would remain on the bank and watch the calves for varying periods of time.

Additional preliminary data (other than the observed predation events) that are based on back-tracking also strongly suggested predation by coyotes on ungulates. Coyote predation on elk and mule deer during the winter months appears to be a function of increased vulnerability: snow conditions and slope (S. Grothe and E. Gese pers. obs., G. Green, pers. commun., 1988) and the size and condition of short-yearlings and adults. During carcass surveys conducted on the northern range in 1987 (Knight et

al. 1988) 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. Mean elk calf mortality reported above was 15%. Crudely extrapolated to the northern range, fifteen percent of, say, 6000 elk calves is 900 elk removed by coyote predation on calves 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 a 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.

BETA PACK MEMBERS AND PUP REARING

Kezha Hatier completed her field work and data collection in August 1993. She and field assistants collected more than 850 hours of field observations on how beta pack members assist in the survival and pup rearing during 1992 and 1993. Her data includes observations on 10 coyote packs. Hatier is currently analyzing data, and completing course work.

Hatier has determined that mean litter size in 1992 was approximately 6.9 pups compared to 3.8 in

1993. Necropsies determined that many pups died of parvovirus in 1992. However, no parvovirus was evident in 1993. This could be because of the relatively cool wet summer in 1993 and the fact that fewer pups were implanted, hence were not found immediately after death.

Den observations revealed that beta pack members bring food to the den for the litter, as well as regurgitate to pups. Betas also protect den sites through chasing and fighting with intruders.

CARCASS USE BY COYOTES

Scott Grothe, a Ph.D. student at Montana State University, is currently collecting data during his last field season in Yellowstone National Park. His dissertation is on winter carcass use by Yellowstone coyotes and its influence on social and population parameters.

Coyote behavior and ungulate mortality data were collected on 61 carcasses (including eight that were translocated from outside the Lamar Valley and Blacktail Plateau study areas) on the northern range between December 1992 and April 1993. During this same time, coyotes at carcasses were observed for 378 hours over 62 days.

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.

◆　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 and roadkill. However, there is a high incidence for canine distemper virus and canine parvovirus. 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,

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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.

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