

Carnivores in Ecosystems: The Yellowstone Experience

Edited by Tim W. Clark
A. Peyton Curlee
Steven C. Minta
Peter M. Kareiva

PRESCOTT COLLEGE LIBRARY
PRESCOTT, AZ.

Yale University Press
New Haven and London

Coyotes and Canid Coexistence in Yellowstone

Robert L. Crabtree and Jennifer W. Sheldon

Adolph Murie's (1940) pioneering work on the ecology of the coyote (*Canis latrans*) in Yellowstone National Park was a landmark of predator research in North America. The Greater Yellowstone Ecosystem (GYE) was to become a major center of carnivore research, and many classic studies followed his lead (e.g., Craighead 1979, Clark 1994), including additional research on coyotes (Robinson and Cummings 1951, Camenzind 1978, Bekoff and Wells 1986). By the late 1980s Yellowstone National Park had undertaken long-term studies of ungulate-killing carnivores, such as the grizzly bear (*Ursus horribilis*, Chapter 3) and mountain lion (*Felis concolor*, Chapter 4), but not the coyote. Because gray wolves (*Canis lupus*) were about to be restored to the park and because the coyote is the most abundant ungulate predator and a major competitor with the wolf, an intensive long-term study of coyotes began in 1989 on the Northern Range of Yellowstone National Park.

Coyotes are ideal carnivores to study because of their ability to adapt and thrive in diverse environments and because of their variable social behavior (Bekoff and Wells 1986). From loose pairs (Berg and Chesness 1978) to packs of ten or more (Crabtree and Varley in press), the mid-sized coyote displays many of the behavioral characteristics seen among the thirty-five species within the family Canidae (Sheldon 1992). Canids themselves are instructive groups through which to examine the community structure of carnivores because of

their wide distribution and variable behavioral and ecological adaptations (Johnson et al. 1996).

This chapter is divided into two sections. The first is a review of major ecological studies of the coyote. Based on these studies, we develop a synthetic view of the coyote from an ecosystem perspective focusing on controversial themes, recent findings, and sociodemographic population limitation issues. The second section examines canid coexistence and competition because it is the least understood, least studied, and possibly most important aspect of coyote ecology. After a brief historical review of Yellowstone's three canids, we discuss the coyote's ecological role in Yellowstone. In striving to understand how canids, and ultimately carnivores, coexist, we focus on the coyote because of its pivotal role, competitively positioned in size between the red fox (*Vulpes vulpes*) and gray wolf. In order to develop a general theory of canid coexistence, we then review sympatric studies of two or more canid species. Our findings are placed in a theoretical framework and applied to a general scenario of three different-sized coexisting canid species typical on other continents. We end with conservation, management, and research recommendations.

The Ecology of Coyotes from an Ecosystem Perspective

In review of past and current field studies of the coyote, we chose eleven study sites based on both study duration and their inclusion of both social-behavioral aspects and population dynamics (table 6.1). Although autecological in nature, most of these studies include the work of two or more projects over two or more time periods, sometimes in two or more areas within the study sites. This allows us to take more of an ecosystem perspective by treating these studies as a continental metapopulation through space and time. For example, the pioneering work of F. Camenzind, M. Bekoff, J. Weaver, and W. Tzilkowski all occurred in close proximity to one another and is lumped together under the heading Jackson Hole, Wyoming.

Carnivores are notoriously difficult to study, so the emphasis of a particular project is often technique dependent. Studies focused on behavioral ecology (for example, Jackson Hole, Wyoming, and in Yellowstone) utilize direct observation, while studies of spatial organization and estimation of demographic parameters (for example, south Texas brushland and northern Utah) usually require intensive capture and radio-tagging efforts. A thorough understanding of long-lived carnivore species and, more important, the coexistence of carnivore communities requires a long-term approach, including direct observations of these behaviorally complex species (Frame 1986). Without such observations, inferences regarding social organization, social structure, and social interactions are suspect (Bekoff and Wells 1986) and can produce er-

roneous conclusions (Waser 1974). Extensive and systematic behavioral observations were conducted only in the Jackson Hole, Wyoming, and Yellowstone field studies.

Another hurdle in synthesizing information across North American coyote studies is the variable and sometimes large effect of human exploitation on the results of field studies. Human exploitation is here defined as human-caused mortality. Although several studies appear to have light exploitation rates, only two (southeast Washington and Yellowstone) examine the unexploited condition. Because of the substantial impact of exploitation on coyote behavior and demographics, we provide subsections to help interpret how coyote populations actually operate under unexploited and undisturbed conditions, thereby gaining valuable insight into the conditions under which they evolved.

FOOD-PREY RELATIONS

Predator-prey relations are best understood from the simultaneous study of both predator and prey (Errington 1935). Fortunately, the first monographical studies of coyotes did focus on prey populations, including a twenty-four-year study in northern Utah and a twelve-year study in central Alberta (table 6.1). Both sets of studies demonstrated the significant influence of coyotes on cyclic populations of snowshoe hares (*Lepus americanus*) and black-tailed jackrabbits (*Lepus californicus*). Even more profound were the functional and the numerical effects of varying prey abundance on coyotes. Strong functional responses are expected when a classic habitat generalist-feeding generalist like the coyote preys on a relatively large, easy-to-handle prey source (see Chapter 9). Strong numerical responses should also occur, given the behavioral plasticity and high reproductive capability of coyotes. When examined, reproductive parameters do respond to major increases or decreases in food supply (Clark 1972, Knudsen 1976, Todd et al. 1981). Few vertebrate mammals the size of coyotes and wolves have the reproductive potential to produce five to eight young per year.

Recent studies tend to focus more on population and behavioral ecology and less on food-prey relations. However, current work in Yellowstone has examined the ecology of coyote predation on small mammal populations (Gese et al. 1996a,b), as did studies conducted in Jackson Hole, Wyoming, during the 1970s (table 6.1). Studies of coyote food habits are numerous but provide unreliable information regarding prey impacts because of sampling biases related to differential digestibility and inconsistent analysis methods (Kelly 1991). Nevertheless, food habit studies indicate that coyotes rely primarily on small mammal prey. Major exceptions appear to be seasonally abundant foods such as fruits in some southern regions, and carrion in northern regions.

WESCOOT COLLEGE LIBRARY

Table 6.1
Comparison of coyote studies

Study site	Period	Food-prey relations
Northern Utah	1963-86	Functional and numerical response to cyclic prey abundance (jackrabbits). Coyote abundance correlated with jackrabbit abundance.
Central Alberta	1964-75	Functional and numerical response to cyclic prey abundance (snowshoe hare). Overall positive correlation between coyote and snowshoe hare abundance.
Jackson Hole, Wyoming	1970-82	Spring abundance correlated with carrion availability. Various aspects of behavior and population demography related to prey resources (carrion and rodent availability).
Southwest Alberta	1974-77	Pack size related to percent of mule deer (not elk) in the winter diet. Functional feeding response with mule deer density and winter killed elk.
South Texas Brushland	1974-82	Not addressed in this study
Southeast Idaho	1975-86	Territory size not related to food abundance but higher proportion of transients during prey scarcity.
South Texas Plains	1978-82	Found no relations between group size and prey size.
Maine	1979-84	Low prey densities may preclude delayed dispersal, resulting in lower pack size.
Southeast Washington	1974-88	Heavy predation on mule deer fawns, while rodents accounted for a large portion of seasonal diets.
Southeast Colorado	1983-86	Prey density and habitat features affect territory size.
Yellowstone	1937-39 1946-49 1989-95	Functional response to seasonally available prey. Coyotes not limiting ungulate populations but are major elk predator due to high density. Coyotes take large portion of rodent prey compared with other predators.

Behavioral ecology

Territory size and percent of transients are related to prey density and exploitation. More juvenile females dispersed, and dispersed farther, than did juvenile males.

Not addressed in this study.

Wolflike social, spatial, and breeding system, including a pack structure. Group size benefits scent-marking and active defense of territories.

Indicates pack formation is an adaptation for efficient capture and defense of ungulate prey. Found a division of labor and evidence of territorial avoidance.

Nonoverlapping territorial core areas. Transients also avoided core areas. Many females ovulate and become pregnant, but only territorial females produce pups.

Spatial use of home range area related to behavior mode, season, temperature, and prey. Avoidance of novel items inside territory but not outside and peripheral.

Exclusive breeding by a territorial female. Alloparental care observed. Movements related to breeding season and not group size or foraging behavior.

Survival rate lower for dispersers than for residents belonging to social groups.

Exclusive breeding by alpha female. High spatially structured social classes. Transient avoided packs. Survival was a function of social class, not age class.

Coyote group size increased with amount of large prey (deer) in the diet. Increased cohesiveness of social groups during breeding season.

Division of labor between alpha male and female. Helping behavior results in more food and defense of pups and higher litter size and survival in good food years. Dispersal by subordinate pack members.

Demographic limitation

Litter size and pregnancy rates correlated with jackrabbit abundance. Winter food limits coyote density during the low period of the jackrabbit abundance cycle.

Snowshoe hare abundance correlated with litter size and reproduction. Carrion abundance related to ingress and egress rates.

Lightly exploited, with territoriality providing spatial limitation of coyotes. Demographic parameters related to food availability, disease, and human-caused mortality.

Not addressed.

Exclusive and successful breeding by territorial females. Immigration of territorial and breeding replacements due to population reduction. Juvenile females dispersed more than males.

Lightly exploited population had low recruitment but high dispersal rates. Spring density not affected by mortality in previous fall-winter period. More females dispersed.

Stable, habitat-saturated population. High pup mortality observed that may be related to disease. A reservoir of transients to replace breeding groups.

No difference between male and female dispersal characteristics.

Unexploited, habitat-saturated population. High pup mortality and dispersal related to social and nutritional stress. Adult survival is 9% for residents and higher for dispersers.

Implied relation between coyote density and prey abundance. Population is habitat-saturated, with large territory size in low prey abundance areas. High juvenile dispersal.

Unexploited, stable, dense, habitat-saturated population. Pack size regulated by neonatal pup mortality and dispersal of subordinates, factors that are related to prey abundance and availability. High adult survival.

continued

Table 6.1
Continued

Study site	Period	Intraspecific competition
Northern Utah	1963-86	Not addressed.
Central Alberta	1964-75	Not addressed.
Jackson Hole, Wyoming	1970-82	Habitat saturation with direct evidence of conspecific killing without consumption. Scent-marking, vocalization, and active defense involved in territorial maintenance.
Southwest Alberta	1974-77	Intrapack dominance hierarchy and interpack spatial avoidance.
South Texas Brushland	1974-82	Implied intraspecific competition based on intrapack spatial avoidance.
Southeast Idaho	1975-86	Implied intraspecific competition based on nonoverlapping home ranges of adults.
South Texas Plains	1978-82	Implied intraspecific competition based on nonoverlapping territorial packs.
Maine	1979-84	Implied intraspecific competition based on nonoverlapping home ranges of adults.
Southeast Washington	1974-88	Intraspecific strife inferred from non-overlapping territories, active defense, and vocalization playbacks. Intruders often identified from olfaction and vision.
Southeast Colorado	1983-86	Implied intraspecific competition based on contiguous, nonoverlapping territories.
Yellowstone	1937-39 1946-49 1989-95	Intraspecific strife inferred by defended, nonoverlapping territories. In poor food years, larger packs produce fewer pups. Territories maintained by physical presence, scent-marking, evictions, and vocalizations.

Interspecific competition**Sources**

Not found or addressed.

Clark 1972, Knudsen 1976, Hoffman 1977, Hibler 1977, Davison 1980, Harris 1983, Mills and Knowlton 1991.

Exploitative competition implied between coyotes, lynx, and raptors. A community approach reaching across three trophic levels.

Nellis and Keith 1976, Todd and Keith 1976, Keith et al. 1977, Todd et al. 1981, Todd and Keith 1976.

Not found or addressed.

Weaver 1977, Camenzind 1978, Tzilkowski 1980, Bekoff and Wells 1981, Wells and Bekoff 1982, Bekoff and Wells 1986.

Some evidence of interspecific competition.

Bowen and Cowan 1980, Bowen 1981, Bowen 1982.

Not found or addressed.

Windberg et al. 1985, Knowlton et al. 1986, Windberg and Knowlton 1988.

High diet overlap with red fox but spatial segregation by habitat type. Possible exploitative competition with bobcats.

Davison 1980, Laundré and Keller 1984, Laundré 1981, Green and Flinders 1981, Harris 1983, Mills and Knowlton 1991.

Not addressed but potential exploitative competition with two scavenging vulture species.

Andelt 1985.

Interference competition with red fox. Spatial segregation occurred as coyotes relegated fox to inferior habitats. High diet overlap and exploitative competition with bobcats.

Harrison and Gilbert 1985, Major and Sherburne 1987, Harrison et al. 1989, Litvaitis and Harrison 1989, Harrison 1992.

Not found or addressed.

Stoel 1976, Steigers and Flinders 1980, Springer 1982, Crabtree 1989, Fulmer 1990, Blatt 1994.

Not found or addressed.

Gese 1988, 1989, Gese et al. 1988.

Interference competition with wolves, grizzlies, and mountain lions at carcasses. Mountain lions also act as predators. Spatial and temporal segregation between coyotes and red fox. Coyote is the major scavenger.

Murie 1940, Robinson and Cummings 1951, Crabtree and Sheldon 1995, Gese 1995, Hatier 1995, Crabtree and Varley in press.

The role of ungulate neonates in the early summer diet of the coyote has received surprisingly little attention, given its apparent impacts on the demography of coyotes and its potential to affect ungulate populations. Ungulate neonates are available during early summer, when pups are at maximum growth rates. The major period of pup mortality from disease and starvation occurs immediately after this period, in July and August (Crabtree and Varley in press). Central-place foragers (for example, den-attending adults) are constrained by time—in addition to the energetic demands of provisioning the young with food—and this should result in prey specialization. Thus adult coyotes would be predicted to specialize on large food items (energy maximizers) according to optimal foraging theory (Pyke et al. 1977). Althoff and Gipson (1981) and Till and Knowlton (1983) indicate that provisioning of pups stimulated adults to prey on domestic ungulates. Behavioral observations in Yellowstone and the preponderance of elk calf remains at den sites corroborate the occurrence of prey specialization in June during pup provisioning. Because differential reproductive success and pup survival are apparently directly linked to the timing and availability of ungulate neonates (or other food sources), evolutionary consideration should be given to the related topics of coyote group formation, the timing of reproduction, and antipredator behavior of both wild and domestic ungulates.

Bekoff and Wells (1986) estimated that about 90 percent of the coyote's diet is mammalian flesh. Because ungulate flesh in the diet is usually carrion (Bekoff 1977, Weaver 1977, Houston 1978) and seasonal in occurrence, few studies have investigated coyote impacts on ungulate populations (but see Messier et al. 1986). Coyotes usually kill ungulates that are weak, impaired, domesticated, or starving, but they are certainly capable of killing healthy adults, even elk in Yellowstone (Gese and Grothe 1995, Crabtree unpublished data). Impacts of coyotes on ungulate populations appear to be mainly via predation on ungulate neonates during pup rearing. We know of no study that indicates significant impacts on the adult segment of an ungulate population. However, predation rates on young ungulates can be high (Hamlin et al. 1984). In Yellowstone, coyotes kill more elk calves (neonates and older calves in winter) than do grizzly bears and mountain lions combined (table 6.2) and inflict heavy predation (greater than 80 percent) on radio-tagged antelope fawns (D. Scott 1994, personal communication). Till and Knowlton (1983) experimentally demonstrated that coyotes kill domestic sheep to provide food for young pups.

BEHAVIORAL AND SOCIAL ECOLOGY

The belief that coyotes are more solitary than other similar-sized canids seems to be the result of cultural folklore and biases in field sampling. In con-

Table 6.2

Comparison of predation rates by large predators in Yellowstone's Northern Range

Species	n	Elk predation				Total	Elk biomass	Per capita kill rate
		Neonate calves	Short yearling	Adult winter	Adult non-winter			
Mountain lion ^a	17	35	313	70	193	611	76,150	36
Grizzly bear ^b	60	750 ^c	0	0	few	750+	13,500	13
Coyote ^d	400	750	360-626	20-35	0	1130-1411	66,760	3

^aData from Kerry Murphy, Hornocker Wildlife Research Institute.^bBonnie Blanchard, personal communication, estimated ~60 grizzlies using the Northern Range.^cFrancis Singer, National Biological Service.^dThis study, projected estimates.

trast to gray wolves, coyote pack members rarely travel all together, and field counts of pack size are usually derived from visual counts of traveling individuals in winter. In addition, human exploitation lowers group size and may cause coyotes to become more secretive and nocturnal. The coyote actually fits nicely into the ecological/body weight relations described by Moehlman (1986) for many canid species. Larger canids, like coyotes, are more social and tend to form packs.

Social organization. Coyote populations are explicit in their spatial arrangement and have well-defined social classes. In synthesizing the results of the studies in table 6.1, which include two recent studies (conducted by the authors) of unexploited populations, we modify the classification of adult coyotes originally proposed by Bowen (1978). His classification was adopted by Bekoff and Wells (1986) to describe two distinct adult social class categories—territorial *pack members* (members of a social group) and nonterritorial *loners*. Adults in territorial packs are further divided into the dominant *alphas* or *breeding pair* and their subordinate *betas*. Betas are pups born in previous years that stay in their natal territory (Crabtree 1989). Beta pack members can either be *helpers*, which help with pup-rearing, or *slouches*, which occupy the territorial area and interact with the breeding pair but seldom contribute toward pup feeding, pup rearing, and den guarding (Hatier 1995).

Loners are subdivided into *solitary residents* and *nomads*. The term *transient* has been used in previous studies to describe all nonterritorial coyotes. However, this is inappropriate because a significant portion of coyotes express site fidelity but do not defend the area they occupy. Solitary residents have levels of site fidelity and home range size similar to that of pack members. In contrast, nomads have low site fidelity and range over large areas (fifty to three hundred square miles), presumably in search of a mate and a territorial vacancy (Crabtree 1989).

Solitary residents generally make up less than 15 percent of the population and are the most heterogeneous social class. They are divided into two subclasses: *floaters* and *former alphas*. Floaters tend to be younger (one to three years old), show weak fidelity to an area, and range over a larger area than most older solitary residents. They spend substantial amounts of time on the periphery of several territories and are suspected to be outcasts from one of the adjacent territories (Crabtree 1989). The characteristics of this subclass match those of the roamers described by Bekoff and Wells (1986) and of individuals described by Messier and Barrette (1982).

The second subclass of solitary residents, *former alphas*, consists of older adults (age three and a half to thirteen and a half), with a degree of site fidelity close to a territorial pack member. Evidence presented by Crabtree (1989) indi-

cates that many of these individuals are former territorial alphas. They have noticeable head and facial scars, which are common on breeding males, and evidence of former reproduction is seen on females. A vocalization study by Fulmer (1990) indicated that older solitary residents occasionally respond to territorial group yip-howls.

Only Bekoff and Wells (1986) described a social category called *resident mated pairs* that do not defend a territory. We believe that this situation arises infrequently, though we have observed it several times in Yellowstone as a direct result of wolf disturbance (Crabtree and Sheldon unpublished data) or as loose, short-term social bonds between male and female solitary residents (observed twice in southeast Washington, table 6.1).

Territories. From 65 to 90 percent of individuals in a coyote population belong to territorial social groups or packs. Territories are defended and are stable in unexploited and lightly exploited areas. They are typically around ten square kilometers and range from about two square kilometers in southern regions (south Texas, table 6.1) to around twenty square kilometers in northern regions (Bowen 1978). Home-range analysis indicates some overlap between territories, but we believe that this could simply be an artifact of the statistical method employed. Observation of scent-marking and territorial defense in Yellowstone indicates relatively little, if any, overlap between groups (Crabtree unpublished data). Statistically defined territorial core areas do not show any overlap in the studies reviewed.

Territory size can vary inversely with prey abundance in other species (Hixon et al. 1983 for birds, Mares et al. 1982 for small mammals), but this relation is not consistent in coyotes (Mills and Knowlton 1991). It is implied for coyotes in southeast Colorado (Gese et al. 1988), but habitat saturation of contiguous, nonoverlapping territories (for example, Yellowstone, south Texas, southeast Washington, table 6.1) may not allow territories to expand and contract with changing prey densities. In addition, the Yellowstone and southeast Washington studies showed a six-year average period for alpha pairs residing in territories.

Sociality, cooperative foraging, and delayed dispersal. The formation of packs, or sociality, in coyotes has been attributed to increased foraging efficiency (see Bekoff and Wells 1986), but this relation, though it has received significant attention, remains unclear. Messier and Barrette (1982) provide an excellent discussion of the subject. Bowen (1981) concludes that group formation in coyotes is an adaptation for the efficient capture of ungulates or economic defense and consumption of carcasses. This hypothesis appears to be supported by other fieldwork (Camenzind 1978, Bekoff and Wells 1986, Bowyer 1987, and for gray wolves, Packard and Mech 1980). Sheldon (1992) questions whether successful

hunting is a secondary effect, as implied by Gese et al. (1988), while Messier and Barrette (1982) provide criticism and compelling alternative hypotheses.

We agree with Messier and Barrette (1982) and find no empirical evidence to demonstrate that larger social groups lead to increased per capita food intake in coyotes. In fact, single individuals and groups of two commonly take down and kill both deer (*Odocoileus* spp.) and elk (*Cervus elaphus*), but larger groups can also be involved (Gese and Grothe 1995, Crabtree unpublished data). This illustrates one of the major problems in evolutionary ecology: are the observations an effect or an evolutionary cause?

Messier and Barrette (1982) propose that group formation in coyotes is the result of delayed dispersal and that exploitation of ungulate prey is a secondary effect. Juveniles that forgo dispersal accrue a variety of benefits, such as secure foraging, increased survival, continued learning, and the attainment of alpha status within or adjacent to their own territory. In addition, delayed dispersal may also be the result of habitat saturation—no vacancies for dispersing juveniles (Davison 1980). Movements of radio-tagged juveniles in Yellowstone and southeast Washington indicate that some juveniles disperse in fall or early winter, but return to their natal territories later in the winter or in the spring before whelping (Crabtree unpublished data). The additional contention by some authors that delayed dispersal may be additionally related to delayed sexual maturity appears weak (Bekoff 1977, Messier and Barrette 1982). Evidence suggests that all females are capable of breeding at ten months of age and that variation in reproductive statistics (for example, age at breeding, percentage of yearling females reproducing) is caused by socially mediated breeding suppression and exploitation effects.

Could delayed dispersal, along with cooperative foraging, be an effect rather than the cause of sociality? We believe that the existence of coyote packs may have evolved along two lines. First, the delayed dispersal hypothesis described above does not necessarily convey a benefit to other related pack members and also delays the time of first reproduction. In fact, delayed dispersers or betas come with an inherent cost to the reproducing pair and their pups—they deplete food resources within the territorial foraging area. Data from southeast Washington and Yellowstone clearly indicate the existence of slouches, beta individuals that do not appear to help the alpha pair with pup rearing. Betas (especially juveniles) are often denied access to winter food and subsequently disperse (Gese et al. 1996b). However, if staying in the natal territory increases a beta's chance of survival and later reproductive success, then from an inclusive fitness standpoint, the dominant alpha parents should tolerate it. Older juveniles and young yearlings (ages nine to fourteen months) have been observed successfully eliciting regurgitations from the alphas with

pups at the den. Thus delayed dispersal may be a form of extended neotony in coyotes when certain ecological conditions dictate a "staying" strategy. Furthermore, a dominance hierarchy provides an efficient social mechanism to regulate a subordinate beta's dispersal. Dominant individuals, i.e., alphas, may assess ecological information, such as low prey abundance or large pack size, and force dispersal of subordinates.

We term the second catalyst for pack formation the pup protection hypothesis, which is similar to that described for lions in Africa (Packer et al. 1990). Under this hypothesis genetic fitness (and a beta's inclusive fitness) is increased if helping actually increases pup survival. Selection pressure comes in the form of pup predation by conspecifics (neighboring packs), predators (golden eagles and bears), and competitors (wolves and mountain lions). In Yellowstone we have observed golden eagles capturing coyote pups at the den, wolves killing coyote pups, and nearly forty instances of den-guarding adult coyotes chasing off both conspecifics and other large carnivores that approach dens. We have also observed adult coyotes chase and attack bears and mountain lions. Camenzind (1978) twice saw adult coyotes from an adjacent territory killing pups at the den site while attending adults were gone. Bekoff and Wells (1986) report that larger groups of coyotes (additional betas) were more effective at chasing off intruders. Hatier (1995) found that larger pack sizes (those with beta helpers) resulted in more den guarding and more food provisionings for pups.

The delayed dispersal and pup protection hypotheses are not mutually exclusive. Because some betas help and others are slouches, it could be that helpers tend to be dominant and add to pack size via pup protection and delayed dispersal, whereas slouches tend to be subordinate and add to sociality via delayed dispersal only. Under this unified hypothesis, a core of one or two helpers is essential. Additional pack members tend to be slouches and are added if beneficial ecological conditions prevail (probably prey abundance). Additional field data are needed to test these hypotheses.

DEMOGRAPHIC LIMITATION

Among the numerous studies of coyote population demographics, only Knowlton (1972) and Knowlton and Stoddart (1983) have attempted a synthetic review regarding the regulation and limitation of coyote populations. In addition to the population mechanics they describe, it is clear that incorporation of coyote social class dynamics, behavior, human exploitation, and competition is essential to any synthesis.

Reproduction and neonatal survival. Female coyotes are monestrous, and the alpha pair mates once a year. Like wolves, coyote packs occasionally produce a

BRUNSWICK COLLEGE LIBRARY

double litter (two breeding females in one pack). We have observed this several times in Yellowstone and estimate that double litters occur 4 percent of the time. In one case, an eleven-year-old alpha female had seven pups, while her daughter, a two-year-old beta female, had a litter of five pups. All pups were communally nursed and reared. The beta female had been a den helper the previous year and appeared closely associated with her alpha female mother.

Litter size at birth appears relatively invariant with respect to changes in prey abundance. Litter size averages about six pups per year and an even sex ratio is common (Bekoff 1977). Numerous studies, spanning a variety of habitats, prey abundances, and exploitation rates, report litter sizes, taken from den counts, between five and seven (Sheldon 1992, Crabtree unpublished data, and see various studies, table 6.1). Even with drastic, ten- to fortyfold changes in jackrabbit and hare abundance, litter size varied only from 6.6 to 7.6 (unborn fetus counts, Clark 1972) and 4.3 to 6.0 (placental scar counts, Todd et al. 1981) in northern Utah and central Alberta, respectively.

Contrary to Knowlton (1972), litter size at birth also appears largely unaffected by levels of human exploitation. He reported an inverse relation between an abundance index (number of coyotes caught per standard trap line in the fall) and litter size varying from 4.3 to 6.9. However, the litter sizes reported from den counts varied only from 5.0 to 5.7. Based on examination of female reproductive organs, he then inferred litter sizes in seven south Texas counties to be 2.8 and 4.2 in a lightly exploited area, 3.7 and 5.3 in a moderately exploited area, and 6.2, 6.3, and 8.9 in an intensively controlled area. It appears that these data have led to the commonly held notion that litter size at birth increases when populations are exploited.

We disagree with the contention of density-dependent adjustments in litter size for several reasons. First, the average litter sizes (den counts) for the two unexploited studies (southeast Washington and Yellowstone, respectively) were 5.6 and 5.4 for successful females. However, 27 percent and 14 percent of alpha females (mostly old-aged) failed to produce pups successfully, and thus the corrected values are 4.1 and 4.5 pups per alpha female in the southeast Washington and Yellowstone studies, respectively. Interestingly, both studies found that radio-tagged alpha females without pups at den emergence time (den counts) all showed localized movements near traditional denning areas at the time of birth (early April). Furthermore, intensive visual observation and capture of two of the reproductively failed alpha females in May revealed evidence of lactation. Thus unsuccessful alpha females appear to have become pregnant and probably lost entire litters shortly after birth (see Sayles 1984). This was first suspected by Knudsen (1976) in northern Utah.

Second, reproductive data gathered from the examination of female car-

cases of unknown social status appear to be misleading. In a particularly enlightening study, Knowlton et al. (1986) radio-tagged sixty-five females to determine age and to classify them as territorial or transient based on intensive monitoring. Females were then collected to examine their reproductive organs. Yearlings, both territorial and nonterritorial, did not ovulate or implant. Fifty percent of the nonterritorial females age two and older ovulated, and 25 percent implanted. None of these ovulating and implanted females successfully whelped. In addition, beta females may have also ovulated and implanted. Thus a much higher percentage of females initiate reproduction than are ever successful. Obviously, this casts serious doubt on the reliability of unborn fetus and placental scar counts being used to infer litter size, let alone successful reproduction. It is also interesting to note that two of four solitary resident females recovered by the authors during spring periods had four and eight embryos in the process of resorption. We have also repeatedly seen various loner females and beta females in copulatory ties during February.

Third, it appears that litter survival (mortality from birth to early winter), not litter size at birth, is the major reproductive parameter that responds in a density-dependent manner to human exploitation. Canids place relatively little energetic investment in gestation, compared with lactation and provisioning of pups during the pups' maximum growth period. Field data collected by the senior author suggest that intraspecific strife leads to alpha females that are in poor condition. Consequently, pups that are born underweight may have inadequate food-provisioning rates, and are predisposed to disease, the proximate cause of mortality (Crabtree 1989 and unpublished data). In Yellowstone mortality appears to affect pups according to a dominance hierarchy already formed by ten weeks of age (Knight 1978). This results in a skewed sex ratio favoring males because males tend to be dominant over females and may gain more access to nursing and regurgitated food.

In studies of unexploited and lightly exploited populations, females first attain alpha status and initiate reproduction when two to five years of age. The probability of successful litters decreases around age seven (Crabtree 1989, Crabtree and Varley in press). Socially sterile beta females, combined with a reservoir of loner females, provide a high potential for replacement of breeding females in exploited populations. In Yellowstone only 35 percent of the females in the population are alphas, of which 86 percent successfully have pups. As a population becomes exploited, it has been reported (Connolly and Longhurst 1975) that as many as 90 percent of females breed. Unless territory size significantly shrinks, these levels are inconsistent with the coyote's classic land tenure system of nonoverlapping territories with one female breeding per territory. Unless exploitation levels are so high as to break down this sys-

tem, such as that described by Berg and Chesness (1978), it is difficult to imagine levels above 66 percent. All studies examining female reproduction have reported territorial and nonterritorial females that do not breed.

Dispersal. We agree with Knowlton and Stoddart (1983) that dispersal is the primary mechanism for maintaining population densities near saturation levels. Davison (1980) and the two studies of unexploited populations clearly indicated emigration from habitat-saturated areas. This serves to reduce population density or to lessen intraspecific competition in the case of a food shortage (Harrison 1992). These studies also indicated lower survival rates for dispersers than for residents. Low survival of dispersers, locally abundant prey, and lack of territorial vacancies in local and nearby areas appear to be selective conditions favoring delayed dispersal (natal philopatry).

In the case of a density-reducing event, a reservoir of loner replacements colonizes vacancies. There is intense competition for vacant territorial areas because newly mated pairs are able exclusively to reproduce successfully, thereby directly increasing fitness. Although loner and beta females occasionally become pregnant, it appears that at least 95 percent are unsuccessful in producing pups. This, combined with the dispersal potential of coyotes (see Robinson and Cummings 1951), suggests that immediate colonization occurs whereby loners and betas intensively compete for territorial residency and the chance to successfully breed. Observations in southeast Washington and Yellowstone indicate that vacated territories act as immigration sinks. Immediate colonization occurred by loners and betas from adjacent packs. In four of ten replacement events, it took one and a half to two years for a new breeding pair to emerge and reproduce. This delay appeared to be the result of intense competition between adults and adult pairs trying to establish pair bonds. In contrast, some territorial vacancies are immediately replaced by a new breeding pair without skipping a successful breeding season.

Evidence gathered in southeastern Washington and Yellowstone (Crabtree 1989, Crabtree and Sheldon unpublished data) indicates that some loners are semidispersed pack members that occasionally visit their natal pack. These individuals are one to four years old and float throughout a large area (for example, 50 km²) surrounding their natal pack. We suspect that intraspecific competition for food within the natal territory results in the semi- or distant dispersal of nonalpha pack members. This allows for efficient reduction of pack size, and more food is available for the remaining dominant adults. Reduction in pack size can result in increased survival for pups as demonstrated by Crabtree and Varley (in press). This loose affiliation may also explain the high proportion of loners in some populations. Mills and Knowlton (1991) proposed that food shortages cause an increase in the proportion of nonterritor-

ial individuals (loners). A mechanistic explanation of how these loners might be derived is provided by Gese et al. (1996b), who describe the dispersal of subordinate pack members that had decreased access to food sources.

Adult survival. Data from the two unexploited coyote populations reported a 9 percent and 10 percent annual adult mortality rate, with occasional vehicle collisions accounting for half of these losses. This is far less than the 40 percent mortality rate assumed by Knowlton (1972) in the absence of exploitation. With Knowlton and Stoddart (1983) calculating that 89 percent of mortalities are attributable to humans, they must have been assuming that human exploitation largely substituted for natural mortality. Even some exploited populations have annual adult mortality rates less than 40 percent (e.g., Windberg et al. 1985). In the absence of exploitation either from humans, predators, or lethal competitors, the major mortality period for coyotes is from birth to six months old. Once a coyote reaches its first winter, the probability is high that it will reach old age.

ASSESSING HUMAN EXPLOITATION

Frank (1979) called for studies of unexploited coyote populations in order to understand the evolutionarily significant situation. Unfortunately, only a few studies, like Camenzind (1978), have been conducted on lightly exploited populations, and only two studies have documented unexploited populations (Crabtree 1989, Crabtree and Varley in press). Nearly all field studies of coyotes have been conducted on populations subjected to substantial levels of exploitation. The results of these studies are thus biased because of the effects of exploitation. For example, coyotes are reported to show flexibility in their social system (Lott 1984). Could such social flexibility be the result of human exploitation, and to a lesser extent, unnatural and human-disturbance conditions? Various studies of coyote populations, all subjected to various levels of exploitation, report significant variation in both social and spatial organization (Berg and Chesness 1978, Camenzind 1978, Danner and Smith 1980, Bowen 1981, Messier and Barrette 1982, Andelt 1985, Bekoff and Wells 1986).

We conducted a survey of coyote radio-telemetry studies in order to assess the effects of human exploitation on coyote populations and the extent to which exploitation clouds our understanding of how coyote populations operate under natural conditions. From this review (R. Crabtree and M. Matteson unpublished data), we constructed sociodemographic scenarios according to three levels of adult coyote exploitation. This subject is obviously complex, and we present these levels so that scientists, managers, and conservationists can understand and interpret these effects better.

Level 1. Unexploited to lightly exploited (0-24 percent annual human-

related mortality). These populations are characterized by stable to fairly stable, habitat-saturated, nonoverlapping territories with boundaries that are stable across time. Pack formation and delayed dispersal is apparent with one to eight subordinate betas depending on prey abundance and proximity to exploited areas that function as dispersal sinks. Pup survival is low (20–60 percent), and few, if any, yearlings reproduce. Average age of adults is three to four years, and the territorial residency time for alpha pairs is three to six years.

Level 2. Moderately exploited populations (25–49 percent annual human-related mortality). These populations are characterized by high turnover of alpha pairs (one to three years). There is a 10–20 percent reduction in population density resulting from decreases in pack size, rather than decreases in number of territories. The land tenure system is intact but has an unstable system of nonoverlapping territories with shifting boundary areas—the population is in a state of semicolonization from immigrants. Some yearling females successfully breed because of a shortage of older, mature females. Pup survival varies from 50–90 percent according to prey resources. Average age of adults is about two years old, and the territorial residency time for alphas is one to three years.

Level 3. Highly exploited populations (50 percent or greater annual human-related mortality). These populations are characterized by an unstable social and spatial system. Individuals have a low probability of surviving until age two. Many yearling females breed because of low competition. Litter size is slightly elevated and pup survival is high, averaging 70–100 percent annually. Packs of three adults are uncommon, with most breeding groups made up of the single breeding pairs. Evidence of loose pair bonds and occasional polygynous breeding events may occur. The age structure includes more than 50 percent yearlings, and the population is in a constant state of colonization with high immigration rates.

Sociodemographic population regulation. Various sociodemographic factors that can regulate coyote populations have been identified—territoriality, dominance hierarchies, breeding longevity, subordinate dispersal, reproductive failure, double litters, and pup mortality. Most studies reviewed indicate direct or indirect evidence of intraspecific competition. Unexploited and habitat-saturated populations indicate intraspecific strife (see Packard and Mech 1980) and a higher level of intraspecific competition. Manifestations include 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. Access to prey has been linked to every major social and demographic event. Crabtree (1989) reported that the population unit on which natality and

mortality primarily act is not age but social class. We agree with Knowlton and Stoddart (1983) that social intolerance, mediated by the abundance and availability of food, is the primary determinant of coyote density. However, recent research indicates that the role played by social behaviorally mediated access to prey has been previously underestimated and that human exploitation common in most field studies has severely confounded our understanding of coyote populations. Long-term studies of coyotes in unexploited and lightly exploited areas, especially when combined with systematic visual observations, have proven irreplaceable in their contribution to a general understanding of coyote ecology.

The one factor that has largely been ignored in coyote research agendas is the role of interspecific competition (but see Keith et al. 1977, Paquet 1989, and Maine, table 6.1). Coyotes coexisted with the competitive pressures of gray wolves over much of their distribution before European settlement. Hence inference regarding the evolutionary mechanisms of coyotes must be taken with caution because most studies were conducted in areas without wolves and other coevolved competitors. An example of the importance of interspecific competition in limiting coyote populations comes from recent data in Yellowstone (Crabtree and Sheldon 1996, Crabtree and Sheldon unpublished data). Wolf killing of coyotes in Yellowstone's Lamar Valley from 1996 through 1998 has resulted in a 50 percent sustained reduction in coyote density. Numerically, this reduction is accounted for by a decrease in pack size as well as a reduction in the number of territorial coyote packs. Either wolves kill alpha coyotes, causing pack disintegration and dispersal, or packs are relegated to an adjacent area. In either case, coyote packs fail to recolonize vacated territories in the high-use areas of a wolf territory. For the above reasons, interspecific competition, specifically canid coexistence, is thoroughly examined in the second half of this chapter.

Coyotes and Canid Competition

In contrast to intraspecific competition, we know very little about the effects of interspecific competition on coyote populations. In order to understand the role of interspecific competition in coyote and canid communities, we provide a brief review of the history of canids in the GYE and the general ecological role of the coyote before wolf restoration. We then examine sympatric canid studies and place them into a theoretical framework applicable to the three canid species present in Yellowstone.

Interference competition—including fighting, killing, direct displacement, and relegation to inferior habitats—has been clearly demonstrated in previous studies, yet wolves, coyotes, and red fox persist in sympatry. Wolves

PRESCOTT COLLEGE LIBRARY

are able to exclude coyotes (Peterson 1996), and coyotes are able to exclude red foxes (Harrison et al. 1989, Sargeant et al. 1987) at various scales, from individual encounters and territories, to entire regions, yet they coexist in many regions of North America. We are therefore particularly interested in the mechanisms of coexistence.

BACKGROUND AND HISTORY OF CANIDS IN THE YELLOWSTONE ECOSYSTEM

Based on the pre-European distribution of the red fox (see Aubry 1983), coyote (Bekoff 1977), and gray wolf (Mech 1974), the red fox and coyote have greatly increased their range across North America while wolves declined substantially during the century-long predator eradication era beginning in the 1860s. All three species occurred naturally in the Cye and the Northern Range of Yellowstone (see also Chapter 2) and coexist once again with the reintroduction of gray wolves in 1995 (see Chapter 5).

The increase in red fox distribution into the lower forty-eight states has been attributed to intentional introduction from Europe and widespread habitat changes accompanying agricultural development (Sheldon 1992). The European red fox inhabits agricultural and human-disturbed habitat at lower elevations, while the red fox endemic to North America resides in either the high-elevation montane-alpine zones of the Rockies, Sierra, and Cascade mountain ranges or the boreal forests of Canada and the Great Lakes states (Crabtree 1993).

The majority of the coyote's range expansion occurred during the predator eradication era (1860s to 1960s), which resulted in drastic reductions in the range distributions of many carnivores. Besides its famed resiliency to predator control techniques, the coyote's range expansion has been attributed to widespread reduction in the distribution of the gray wolf and the clearing of forests. The coyote now occupies most habitat types in North America, although it is best adapted to the arid and open shrub-grassland areas of the West (Bekoff 1977).

The red fox, adapted to alpine tundra and boreal forest, was certainly present in the Yellowstone region during, before, and after the Wisconsin glaciation. The coyote, however, was probably present in the Yellowstone region only during interglacial periods and possibly during glacial periods in the lower elevation areas surrounding the ice-capped mountains. The gray wolf probably inhabited only areas of boreal forest to the south of ice sheets, where ungulate populations supported breeding populations, and moved into the higher elevations once the continental ice sheet began to retreat.

Schullery and Whittlesey (1992) reviewed historical sightings of canids prior to 1890 and found that sightings of wolves and foxes were common, while

coyote sightings were rather infrequent. Although this could partly be the result of misclassifying coyotes as wolves, it is clear that several park officials were very adept at distinguishing species, even color morphs of red fox (see Norris 1881). The surprising lack of coyote sightings stands in sharp contrast to the trapping records of Skinner (1927) from 1906 to 1927 when the last wolves were extirpated from the Northern Range of Yellowstone. While 127 wolves and 134 mountain lions were killed, 4,356 coyote mortalities were recorded. Even if 80 percent were pups killed at dens (which is doubtful), coyotes appear much more abundant than wolves. This leaves us with a peculiar paradox—where did all the coyotes come from? Were they already there? Could coyote numbers, once released from wolf pressure, have quickly rebounded?

Distribution and abundance of coyotes in the Greater Yellowstone Ecosystem. Currently, the coyote inhabits all vegetation communities below 8,000 feet in the GYE, except for areas of contiguous deep snow and steep rocky areas. Based on extensive winter surveys conducted from 1992 through 1995 (Gehman et al. 1997), the coyote uses all elevations above 8,000 feet, but only on a transitory basis. The typical coyote behavior of territorial establishment, courting, pair-bonding, and breeding that takes place from December through February is absent above 8,000 feet. However, coyotes are commonly observed from 8,000 to 11,000 feet in meadow and mixed forest-meadow habitats from May to July. These coyotes are seen in male-female pairs engaged in courtship and pair-bonding. Nonterritorial coyotes that reside below 8,000 feet during winter apparently travel to these areas in late April and May as snow melts and prey becomes available. These pairs vocalize, scent-mark, and defend territories just like lower-elevation coyotes in winter, but no successful reproduction has been detected.

The estimated density of adult coyotes on the Northern Range averages 0.45 per square kilometer (Crabtree and Varley in press) based on total counts and capture-recapture estimates (Crabtree et al. 1989). In the open, shrub-steppe and mesic grasslands of the GYE, coyotes can reach local densities exceeding one per square kilometer. However, across much of the mixed meadow-forest habitat types of the GYE, coyote densities range from 0.1 to 0.4 coyotes per square kilometer.

Prewolf ecological role of the coyote. The high density of coyotes on the Northern Range adds a strong numerical component to an already broad functional role as a generalist consumer. In this section we compare historical data to current information, estimate biomass consumption of different prey species, and calculate the percentage of prey species removed by coyotes. These data further underline the coyote's stable and broad ecological role on Yellowstone's Northern Range.

Table 6.3

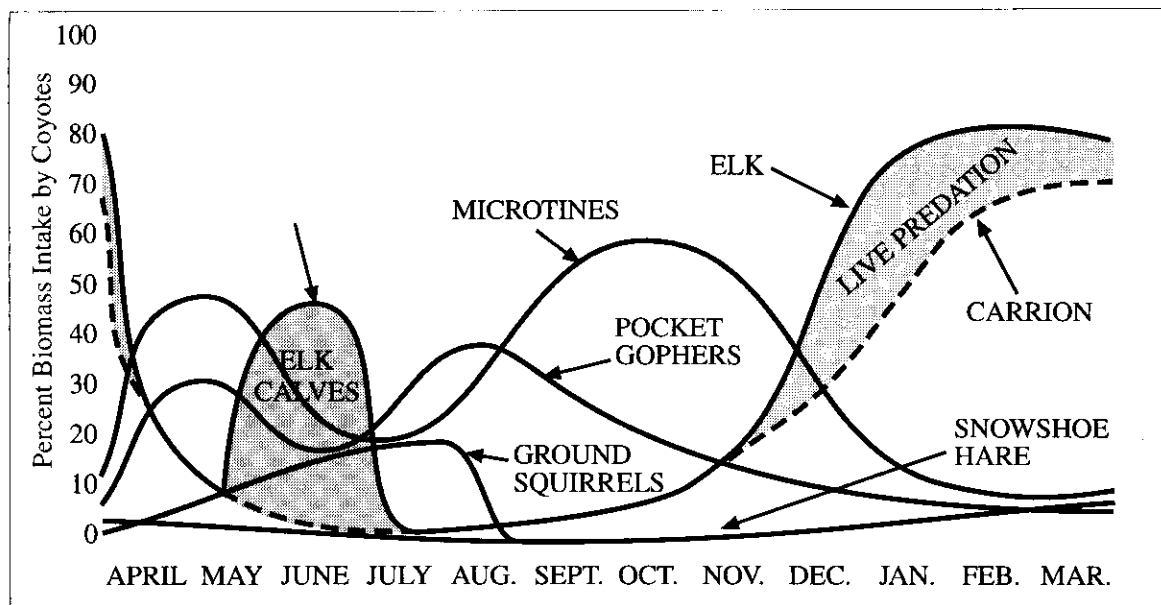
Coyote food habits as indicated by analysis of scats (% of biomass intake)

Prey species	Murie 1940 (5,086 scats)	This study (1995; 500 scats)
<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

The ecological role of the coyote was defined by Murie (1940) from analysis of 5,086 scats. We summarized these data and compared them to a subsample of five hundred scats collected in 1991 and 1992 (table 6.3). The data sets were remarkably similar, indicating stable resource use. This, combined with the apparent stability in the location of traditional den sites, suggests that prey availability and preferences have also been relatively stable. Based on our results, the observations of Murie (1940), and the similarity of den site locations during 1946–49 (Robinson and Cummings 1952) and 1990–94, we believe that the number and location of coyote packs on the Northern Range became stable shortly after the extirpation of the gray wolf in 1927.

The coyote is the major elk predator on the Northern Range, killing an estimated 1,276 elk annually, the majority of which are neonates (table 6.2). The coyote population accomplishes this not by specialization but by sheer numbers (450 coyotes), along with a propensity for killing mostly young neonates (an estimated 750 annually) in June and weak or starving adults during winter. Although coyotes are capable of killing healthy adult elk during winter, they seldom do so (Crabtree unpublished data, Gese and Grothe 1995). In comparison, mountain lions kill around six hundred elk (only thirty-five neonates) and grizzlies kill an estimated 750 neonates and a few adults (B. Blanchard, personal communication). The estimated per capita annual kill rates for an estimated 450 coyotes, sixty grizzly bears, and seventeen adult mountain lions on the Northern Range are three, thirteen, and thirty-six elk, respectively.

Estimates of the biomass of various prey species consumed by coyotes were based on: (1) independent estimates of predation rates (Gese et al. 1996a), (2) carcass consumption rates (S. Grothe unpublished data), (3) observed predation rates on ungulates (Gese and Grothe 1995, R. Crabtree unpublished data), and (4) seasonal estimates of the fresh weight of prey consumed, from scat analysis incorporating differential digestibility corrections (Kelly 1991). Nearly 50 percent of the annual biomass intake came from small mammals (taken mostly in summer and fall), and nearly 45 percent from ungulates taken mostly in winter and spring (figure 6.1). In the seven nonwinter months, microtines made



6.1. Seasonal biomass intake by coyotes in Yellowstone's Northern Range.

up 41 percent of prey biomass consumed, pocket gophers 25 percent, ground squirrels 3 percent, snowshoe hares 4 percent, and elk (calves and carrion) 21 percent. An estimated 74 percent of the biomass intake during the five winter months came from elk (primarily carrion), and 26 percent from small-mammal prey.

The coyote's estimated take of small-mammal prey on the Northern Range is indicative of the high density of the prey and of the coyote's broad functional role. Among fifteen species of carnivores that rely on small-mammal prey as their major food source, the coyote accounts for an estimated removal of 76 percent of the estimated population of microtines, 24 percent of pocket gophers, 35 percent of ground squirrels, and 10 percent of neonate elk calves (Chapter 3, Singer unpublished data). Nearly three-fourths of the elk biomass consumed during the five winter months is carrion, and at least two-thirds of the live predation on elk involves old or starving individuals. As Murie (1940) suspected, harsh winters result in large numbers of carcasses for scavenging coyotes. In mild winters with little carrion, coyotes can lose up to 30 percent of their body weight. The availability of carrion directly affects litter size (Crabtree and Varley in press).

CANID SYMPATRY AND COEXISTENCE

Because they are remarkably diverse, canids are an instructive group through which to examine carnivore competition and the resultant mechanisms of coexistence. Members of this family range in weight from one and a half to eighty kilograms, with variable diets and feeding strategies ranging from insectivory to omnivory to almost complete carnivory. For example, the largest canid, the gray wolf, is an obligate carnivore that specializes in killing ungulates but can seasonally utilize a substantial portion of nonungulate, small-mammal prey in its diet (Crabtree 1992). Life-history traits and social organization are highly variable among the Canidae, as are their adaptability and behavioral plasticity (Sheldon 1992).

In a comprehensive review of canid sympatry, Johnson et al. (1996) examined how resources are partitioned among potential competitors. These authors assessed sympatric canid pairs throughout the world in terms of diet breadth, as well as temporal, spatial, and habitat overlap. A summary follows of canid ecological relations described in Johnson et al. (1996) and a multitude of other studies of sympatric canids (e.g., Chambers 1987, Chypher and Scrivner 1992, Dekker 1983, Dibello et al. 1990, Engelhardt 1986, Gittleman 1986, Green and Flinders 1981, Jimenez 1993, Johnson 1992, Klett 1987, Moehlman 1986, Sargeant and Allen 1989, Sargeant et al. 1987, Theberge and Wedeles 1989, Voigt and Earle 1983, White et al. 1994, Wooding 1984).

Review of the above papers gives rise to generalizations grouped into the topics presented in the following sections.

Size dominance. Species dominance among sympatric canids is universally a function of size: in competitive interactions, larger canid species are dominant over smaller ones. However, numerical advantage in smaller species can sometimes temporarily reverse the direct dominance of the larger species (Litvaitis 1992, Davis 1980, Schamel and Tracy 1986, Dekker 1983, 1989, 1990, Johnson 1992, Jimenez 1993, Paquet 1991, Crabtree and Sheldon personal observations).

Three-species canid pattern. According to Johnson et al. (1996), a pattern of three sympatric canid species occurs in North America, Eurasia, and Africa. This consistent pattern of partitioning based on ecological roles seems to permit canid coexistence (Rosenzweig 1995), but these three species are not the only canids or competing carnivores in many of these regions. In each region, even though the species are different, the three types of canids occur in congruent patterns of functional roles, consisting of: (1) a large (more than twenty kilograms), obligate ungulate killer—for example, African wild dog (*Lycaon pictus*), dhole (*Cuon alpinus*), or gray wolf; (2) a medium-sized omnivore of ten to twenty kilograms—for example, golden jackal (*Canis aureus*) or coyote; and (3) a small, highly omnivorous species—for example, corsac fox (*Vulpes corsac*), fennec fox (*Fennecus zerda*), or red fox.

Disruptions to predator assemblages brought about by the human removal of the largest canid and obligate carnivore are widespread. In Africa the African wild dog, in Asia the dhole, and in North America the gray wolf have been eradicated from regions where human populations conflict with these species. These large, highly social, low density, obligate ungulate predators have proven relatively easy to eradicate. Smaller, omnivorous, generalist canid species are generally more resilient and tolerant of human presence. Their populations often increase following removal of the largest canid, suggesting that competition between the canid species had depressed populations of the smaller canid. Rapid range expansion of generalist canids such as coyotes, red foxes, and jackals often follows these eradications (Sheldon 1992). The ecosystem-wide effects of this rapid range expansion of generalist canids need to be assessed. In some ways these ultrageneralists can be seen as weedy species, the gulls of the dog world.

The predominant diet pattern among sympatric canids is the three-species canid pattern described above; alternatively, in a two-canid system the larger canid is more strictly carnivorous while the smaller is an opportunistic omnivore with significantly greater niche breadth. Diet studies are numerous (e.g., Lamprecht 1978, Dibello et al. 1990, Paquet 1992, Fuller et al. 1989, Johnson and Franklin 1994, Nel 1984, Jimenez 1993, Jaksic et al. 1983, Andriashek et al. 1985,

Brown 1990, Bothma 1971, Bothma et al. 1984, Smits et al. 1989, Hockman and Chapman 1983, Small 1971, Green and Flinders 1981). Niche breadth, prey biomass, prey diversity, and habitat heterogeneity all seem to be important in determining the economies of resource partitioning. In general, little information is available on numerical aspects of canid sympatry; for instance, density or relative abundance ratios. Most of the information on population numbers is derived indirectly from trapping indices.

Spatial and temporal partitioning. There is clear evidence of temporal and spatial partitioning between sympatric canids. In general, the smaller canids avoid the larger ones (Theberge and Wedeles 1989, Paquet 1992, Ingle 1990, Follman 1973, Bailey 1992, Davis 1980, Hersteinsson and Macdonald 1982, Dekker 1983, 1989, 1990, Paquet 1992, Moehlman 1983). Differences in activity patterns do not usually result in decreased diet overlap, but rather may represent behavioral avoidance of potential agonistic interactions with competitors. The same is true for spatial avoidance patterns. The rule of thumb on the part of the smaller canid seems to be avoidance of potentially lethal encounters rather than maximization of energetic intake.

Interference competition. Interference competition between sympatric canid species is common (O'Farrell 1984, Paquet 1992, Berg and Chesness 1978, Carbyn 1982, Egoscue 1956), often culminating in the killing of one canid species by another (Murie 1944, Berg and Chesness 1978, Carbyn 1982, O'Farrell 1984; see Peterson 1996 for a recent review). In fact, the first kill that reintroduced wolves made in Yellowstone was a red fox that climbed into a wolf enclosure. In general, one canid species does not completely exclude another regionally (Johnson et al. 1996). Exceptions to this general rule occur on Isle Royale, Michigan, where the last coyote from an originally robust population was seen seven years after the first gray wolf crossed over to the island on an ice bridge (Krefting 1969), and in California, where coyotes effectively seem to exclude kit foxes across large areas (O'Farrell 1984).

The extent to which high interspecific kill rates among canids are an artifact of colonizing or perturbed populations is not clear. Examination of wolf-caused coyote mortality in Yellowstone National Park should provide insight into accommodations by the two species as wolves approach habitat saturation. As Frame (1986:xxi) points out: "Only the direct observation of interference competition in long-term field studies identified where competitive interactions are occurring with sufficient intensity to provide a numerical response in a population." Observations of direct competitive interactions provide valuable insight into the behavioral and demographic components of coexistence.

Competition imposes energetic costs, affects survival and fecundity, and

may force relegation to less optimal habitats (with lower resource availability or higher risks). The manifestations of interspecies competition can be quite subtle. Follman's (1973) study of sympatric red and gray foxes found little overt evidence of competition, and the two species were segregated by habitat. It can also be less subtle: in South America where the chilla (*Dusicyon griseus*, five kilograms) and culpeo (*Dusicyon culpaeus*, five to thirteen kilograms) are sympatric, the larger canid excluded the smaller from optimal habitat via interference competition, and the chilla was relegated to suboptimal habitats (Johnson 1992). This pattern of spatial relegation of the smaller canid is commonly found in other sympatric canid pairs. Temporal segregation reduces competition for food only if different activity patterns result in access to different prey populations (Pianka 1974) or if food resources are renewed within the period of temporal segregation (Litvaitis 1992).

Character displacement. The carnivore complex in East Africa contains five sympatric canids, the highest density of canid sympatry anywhere, a phenomenon that may in part result from the enormous diversity and biomass of available prey. Van Valkenburgh and Wayne's (1994) study of three sympatric jackals in East Africa brings to light some difficulties with the traditional view of species overlap and its relation to morphological character displacement. The three sympatric jackal species in East Africa (*Canis mesomelas*, *C. adustus*, and *C. aureus*) appear to have converged rather than diverged morphologically and seem to segregate ecologically (Fuller et al. 1989). Similarly, sympatric coyotes and wolves in Ontario appear to be converging in body weight and length (Schmitz and Lavigne 1987).

Home-range interspersions. The geometry of canid home ranges—that is, how they are interspersed and spaced—is important. The few concurrent telemetry studies of canids have shown how the home ranges of smaller canids and their prey fit in between the home ranges of the larger canids. Deer densities are highest in the gaps between the home ranges of different wolf packs (Mech 1977). Similarly, the red fox home ranges in Yellowstone are located between and on the periphery of coyote territories (Fuhrmann 1998). Essentially all of the sympatric studies reviewed that had concurrently tracked two species of radio-tagged canids indicated some degree of home range interspersions or fine-scale allopatry.

Scavenging. In ecosystems where large predators kill more prey than they can consume in one feeding bout, smaller coexisting canids may benefit (see Paquet 1989). This opportunistic scavenging behavior is a function of group size, with unpredictable outcomes. Large social groups of smaller-sized scavengers can usurp kills, and large social groups of top carnivores can keep scavengers away more effectively. Both satiation level and stage of carcass con-

sumption appear to influence the outcomes of interspecific interactions at kills (S. Grother personal communication). Among canids it is clear that sociality functions to protect against scavengers stealing carcasses. Preliminary data from observed wolf-killed ungulate carcasses on the Northern Range suggest that bears, eagles, ravens, and coyotes all benefit from the addition of carion biomass via wolf reintroduction.

MECHANISMS OF COEXISTENCE IN THE GREATER YELLOWSTONE ECOSYSTEM

Based on the review of sympatric canid studies, we hypothesize that canid coexistence is primarily a function of avoiding fatal encounters while attempting to secure or defend the prey necessary to survive and successfully reproduce. Canids therefore employ a variety of behaviors that result in spatial and temporal resource partitioning. Given the historic and prehistoric sympatric distributions, the abundance and consistency of observations reporting aggressive and fatal interactions between coyotes and gray wolves and between coyotes and red foxes imply that they are not rare events and that strong selection pressures occur.

In the Yellowstone ecosystem, as well as other areas of North America, we propose four mechanisms that mediate canid coexistence: (1) simple geometry, (2) individual behavioral avoidance as mediated by sensory perception, (3) Paquet's (1992) scavenger potential hypothesis, and (4) effective social group size.

Simple geometry contends that the disproportionate relation between body size (four, twelve, and thirty-six kilograms, respectively) and territory size (two, twelve, and two hundred square kilometers, respectively) in the red fox, coyote, and gray wolf further facilitates the efficient interspersions of the home ranges of two or more canid species. The smaller canid has relatively more space in between and on the periphery of the larger canid's territory. In addition, the smaller canid likely has a lower probability of encounter with the larger canid. This may be especially true for the red fox, which is relegated to suboptimal habitats by the dominant coyote (Harrison et al. 1989). Red foxes can avoid the core of coyote territories and still survive on relatively dense rodent and insect prey populations.

Behavioral avoidance is based on the highly evolved senses of members of the family Canidae. Avoiding fatal encounters requires detection of the larger canid through visual, auditory, or olfactory cues. In addition, the red fox is highly nocturnal in Yellowstone compared with the more diurnal and crepuscular coyote (Fuhrmann 1998). Both red foxes and coyotes have been observed to wait at distances of two hundred meters to over one kilometer until wolves

have left their kills, thereby temporally partitioning a high-energy food resource during winter.

Scavenger potential was first described by Paquet (1989). This hypothesis is based on the observation of wolves consuming large ungulates over multiple feeding bouts. The smaller canid scavenges on the ungulate carcass between feeding bouts when wolves (or coyotes) are resting for several hours (Paquet 1992). For example, in areas where white-tailed deer (*Odocoileus virginianus*) are the primary prey, packs of wolves can consume a whole deer in one feeding bout, leaving little for coyotes.

Effective group size appears to be an important means of avoiding fatal encounters. Of more than two hundred wolf-coyote encounters observed in Yellowstone from 1996 through 1998 (Crabtree and Sheldon 1996, unpublished data), fifteen resulted in coyote deaths. All deaths involved three or more wolves and a single coyote. Groups of coyotes were also observed attacking single wolves and usurping their kills. Genetically related individuals engage in group defense of a carcass, den site, or open-field encounter with a larger canid. In addition, vigilance (and detection) is often more efficient in a social group. Preliminary analysis of data collected in Yellowstone (A. Gladwin unpublished data) indicate a per capita decrease in vigilance behaviors with increasing group size.

Conservation, Management, and Research Recommendations

COYOTE POPULATIONS

The coyote's distribution across North America has tripled during the past century. Clearly, the coyote does not represent a small-population conservation problem. Nevertheless, restoration of coyotes to some areas may serve a functional role in the conservation of other species. For example, it may be useful to reassess the functional role of coyotes where deer are overabundant, or where red fox populations inflict heavy predation on ground-nesting birds, livestock, or poultry. We believe that conservation science can learn important lessons from understanding a successful and ubiquitous species like the coyote, in addition to the important lessons learned from declining species.

Because of the numerous sociodemographic and density-dependent processes that take place in response to widespread population reductions and indiscriminate killing, federal programs to limit coyote numbers have proven ineffective and costly. Field research is needed to experimentally examine the effectiveness of control and the responses of coyote populations to exploitation. We believe that the coyote's famed behavioral plasticity and demographic

EMERSON COLLEGE LIBRARY

resiliency to exploitation is an evolutionary product of coexisting with competing species, mainly the gray wolf. The proposed fifteen-year study in Yellowstone (pre- and postwolf) should provide this needed information. So far, gray wolves have inflicted heavy mortality on coyotes during the winter in wolf core-use areas (see Crabtree and Sheldon 1996), and the sex and age structure of twenty-four wolf-killed coyotes appears to be relatively indiscriminate, with a possible bias toward younger individuals (much like human trapping efforts).

CANID COEXISTENCE

It is clear that interspecific relations between canid species competing for limited resources can have significant impacts. This has major implications for conservation and management. Medium- and smaller-sized canids have shown a release (Soulé et al. 1988) following a reduction or extirpation of the larger canid (Hersteinsson et al. 1989, Lewis et al. 1993, Peterson 1996). Thus future reintroduction efforts should consider these and other community effects before implementation. Canid hybridization has occurred repeatedly (Lehman et al. 1991, Wayne and Jenks 1991, Boitani 1982, Gottelli and Sillero-Zubiri 1992) and can hamper or complicate expensive reintroduction efforts (Gittleman and Pimm 1991).

We agree with Johnson et al. (1996) that monitoring the effects of canid reintroduction programs provides a splendid opportunity to examine canid community structure and competition experimentally. Furthermore, Yellowstone's wolf reintroduction will provide a unique opportunity to understand such community-wide effects as functional and numerical responses by other small-mammal predators (for example, red foxes, weasels, raptors) responding to significant reductions in coyote populations. Initial estimates of wolf numbers in northern Yellowstone made by Garton et al. (1990) suggest there will be a tripling of the amount of potential carrion available to scavengers, which could have significant impacts on, for example, threatened Yellowstone grizzly bear populations. Changes in elk behavior and distribution followed by subsequent changes in vegetation are yet other possible responses (Chapter 8).

Canids, especially coyotes, display wide-ranging variability in their behavioral ecology and population demography, and thus serve as excellent candidates for understanding carnivore communities. Long-term study, combined with systematic behavioral observation and experimental (and natural) manipulation is required in order to craft successful conservation strategies for communities in dire need of restoration. Such field studies are difficult and pose challenges to agencies, universities, and private organizations that must cooperate in order to plan, fund, and execute these invaluable studies.

Coyotes and Canid Coexistence

Acknowledgments: We thank the staff of Yellowstone National Park, especially John Varley, chief scientist, for support, guidance, and timely advice. A special thank-you to the numerous field technicians, interns, and volunteers who worked on various aspects of the field research, especially graduate students R. Fuhrmann, E. Gese, S. Grothe, K. Hatier, W. Monroe, P. Moorcroft, Deborah Smith, and C. Wilmers. M. Phillips, Douglas Smith, K. Murphy, and W. Brewster of Yellowstone National Park's Wolf Ecology Project provided field and logistical support. We also thank Battelle Pacific Northwest Laboratories, Hanford, Washington, and E. Ables, University of Idaho, for support of the research conducted in southeast Washington under U.S. Department of Energy contract DE-AC06-76RLO-1830. The research in Yellowstone was funded primarily by the National Park Service (1989-94) under cooperative agreement 1268-1-9001 to R. L. Crabtree, and by Yellowstone Ecosystem Studies (1993-99). Additional funding and support was provided by Bob and Dee Leggett, Defenders of Wildlife, Bob Landis of Landis-Trailwood Films, National Geographic Society, World Wildlife Fund, Marian Probst, Earthwatch, Hornocker Wildlife Research Institute, Max McGraw Wildlife Foundation, Greenville Foundation, Turner Foundation, U.S. Fish and Wildlife Service, U.S. Department of Agriculture, U.S. National Biological Service, M. Johnson of Wildlife Veterinarian Services, Biology Department at Montana State University, Department of Wildlife Ecology at the University of Wisconsin-Madison, and J. Williams at University of North Carolina-Wilmington. P. Curlee and S. Minta provided valuable review and comments on earlier drafts.

- Literature Cited:* Althoff, D. P., and P. S. Gipson. 1981. Coyote family spatial relationships with reference to poultry losses. *Journal of Wildlife Management* 45:641-49.
- Andelt, W. F. 1985. Behavioral ecology of coyotes in South Texas. *Wildlife Monographs* no. 94:1-45.
- Andriashek, D., H. P. L. Kiliaan, and M. K. Taylor. 1985. Observations on foxes, *Alopex lagopus* and *Vulpes vulpes*, and wolves, *Canis lupus*, on the off-shore sea ice of northern Labrador. *Canadian Field-Naturalist* 99:86-89.
- Aubry, K. B. 1983. The Cascade red fox: Distribution, morphology, zoogeography, and ecology. Ph.D. diss., University of Washington, Seattle.
- Bailey, E. P. 1992. Red foxes, *Vulpes vulpes*, as biological control agents for introduced arctic foxes, *Alopex lagopus*. *Canadian Field-Naturalist* 106:200-205.
- Bekoff, M. 1977. *Canis latrans*. *Mammalian Species* no. 79:1-9.
- Bekoff, M., and M. C. Wells. 1981. Behavioral budgeting by wild coyotes: The influence of food resources and social organization. *Animal Behaviour* 29:794-801.
- . 1986. Social ecology and behavior of coyotes. Pp. 251-338 in J. S. Rosenblatt, C. Beer, M.-C. Busnel, and P. J. B. Slater, eds., *Advances in the study of behavior*. Academic Press, New York.
- Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pp. 229-48 in M. Bekoff, ed., *Coyotes: Biology, behavior, and management*. Academic Press, New York.
- Blatt, J. W. 1994. Demographics and dispersal of coyote (*Canis latrans*) pups. M.S. thesis, Central Washington University, Ellensburg.
- Boitani, L. 1982. Wolf management in intensively used areas of Italy. Pp. 158-72 in F. H. Harrington and P. C. Pacquet, eds., *Wolves of the world: Perspectives of behavior, ecology, and conservation*. Noyes Publications, Park Ridge, New Jersey.
- Bothma, J. D. P. 1971. Food habits of some Carnivora (Mammalia) from Southern Africa. *Annals of the Transvaal Museum* 27(2):15-26.
- Bothma, J. D. P., J. A. J. Nel, and A. Macdonald. 1984. Food niche separation between four sympatric Namib Desert carnivores. *Journal of Zoology* (London) 202:327-40.
- Bowen, W. D. 1978. Social organization of the coyote in relation to prey size. Ph.D. diss., University of British Columbia, Vancouver.
- . 1981. Variation in coyote social organization: The influence of prey size. *Canadian Journal of Zoology* 59:639-52.

- Bowen, W. D., and McT. I. Cowan. 1980. Scent marking in coyotes. *Canadian Journal of Zoology* 58:473-80.
- Bowyer, R. T. 1987. Coyote group size relative to predation on mule deer. *Mammalia* 51:515-26.
- Brown, G. W. 1990. Diets of wild canids and foxes in East Gippsland, 1983-1987, using predator scat analysis. *Australian Mammalogy* 13:209-13.
- Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pp. 267-94 in M. Bekoff, ed., *Coyotes: Biology, behavior, and management*. Academic Press, New York.
- Carbyn, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. *Canadian Field-Naturalist* 96:176-83.
- Chambers, R. E. 1987. Diets of Adirondack coyotes and red foxes. *Transactions of the Northeastern Section of the Wildlife Society* 44:90.
- Chypher, B. L., and J. H. Scrivner. 1992. Coyote control to protect endangered San Joaquin kit foxes at the Naval Petroleum Reserves, California. Pp. 42-46 in J. E. Borrecco and R. E. Marsh, eds., *Proceedings of the 15th Vertebrate Pest Conference*, Davis, California. University of California, Davis.
- Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. *Journal of Wildlife Management* 36:343-56.
- Clark, T. W. 1994. Restoration of the endangered black-footed ferret: A twenty-year overview. Pp. 272-97 in M. L. Bowles and C. J. Whelan, eds., *Restoration and recovery of endangered species*. Cambridge University Press, Cambridge.
- Connolly, G. E., and W. M. Longhurst. 1975. The effects of control on coyote populations. University of California, Davis, Division of Agricultural Science, Bulletin no. 1872.
- Crabtree, R. L. 1989. Social, spatial, and demographic characteristics of an unexploited coyote population. Ph.D. diss., University of Idaho, Moscow.
- . 1992. A preliminary assessment of the non-ungulate mammal prey base for wolves in Yellowstone National Park. Pp. 5-122 to 5-138 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 Service, Yellowstone National Park.
- . 1993. Gray ghost of the Beartooth. *Yellowstone Science* 1(3):13-16.
- 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. *Journal of Wildlife Management* 53:949-54.
- 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, Mammoth.
- Crabtree, R. L., and J. D. Varley. In press. Ecological and sociodemographic role of the coyote on Yellowstone's Northern Range. *Proceedings of the 3d biennial science conference on the Greater Yellowstone Ecosystem, Greater Yellowstone's predators*, September 24-27, 1995. Yellowstone National Park and Northern Rockies Conservation Cooperative, Mammoth.
- Craighead, F. C., Jr. 1979. Track of the grizzly. Sierra Club Books, San Francisco.
- Danner, D. A., and N. S. Smith. 1980. Coyote home range, movement, and relative abundance near a cattle feedyard. *Journal of Wildlife Management* 44:484-87.
- Davis, G. K. 1980. Interaction between bat-eared fox and silver-backed jackal. *East Africa Natural History Society Bulletin*, September-October, 79.
- Davison, R. P. 1980. The effect of exploitation on some parameters of coyote populations. Ph.D. diss., Utah State University, Logan.
- Dekker, D. 1983. Denning and foraging habits of red foxes, *Vulpes vulpes*, and their interactions with coyotes, *Canis latrans*, in central Alberta, 1972-1981. *Canadian Field-Naturalist* 97:303-6.
- . 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. *Canadian Field-Naturalist* 103:261-64.

Coyotes and Canid Coexistence

- . 1990. Population fluctuations and spatial relationships among wolves, coyotes, and red foxes in Jasper National Park. *Alberta Naturalist* 20:15-20.
- Dibello, F. J., S. M. Arthur, and W. B. Krohn. 1990. Food habits of sympatric coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, and bobcats, *Lynx rufus*, in Maine. *Canadian Field-Naturalist* 104:403-8.
- Egoscue, H. J. 1956. Preliminary studies of the kit fox in Utah. *Journal of Mammalogy* 37:351-57.
- Engelhardt, D. B. 1986. Analysis of red fox and coyote home range use in relation to artificial scent marks. M.S. thesis, University of Maine, Orono.
- Errington, P. L. 1935. Over-populations and predation: A research field of singular promise. *Condor* 37:230-32.
- Follman, E. H. 1973. Comparative ecology and behavior of red and gray foxes. Ph.D. diss., Southern Illinois University, Carbondale.
- Frame, G. W. 1986. Carnivore competition and resource use in the Serengeti ecosystem of Tanzania. Ph.D. diss., Utah State University, Logan.
- Frank, L. 1979. Review of *Coyotes: Biology, behavior, and management*, by Marc Bekoff. *Journal of Mammalogy* 60:658-59.
- Fuhrmann, R. T. 1998. Distribution, morphology, and habitat use of the red fox in the northern Yellowstone ecosystem. M.S. thesis, Montana State University, Bozeman.
- Fuller, T. K., A. R. Biknevicius, P. W. Kat, B. Van Valkenburgh, and R. K. Wayne. 1989. The ecology of three sympatric jackal species in the Rift Valley of Kenya. *African Journal of Ecology* 27:313-23.
- Fulmer, K. F. 1990. Characterizing the functions of coyote vocalizations through the use of playback. M.S. thesis, University of Idaho, Moscow.
- Garton, E. O., R. L. Crabtree, B. B. Ackerman, and G. L. Wright. 1990. The potential impact of a reintroduced wolf population on the northern Yellowstone elk herd. Pp. 3-59 to 3-91 in *Wolves for Yellowstone? A report to the United States Congress, vol. 2, research and analysis*. National Park Service, Yellowstone National Park.
- Gehman, S., R. Crabtree, E. Robinson, M. Harter, and S. Consolo-Murphy. 1997. Comparison of three methods for detecting mammalian carnivores. Final Report to Yellowstone National Park, Mammoth.
- Gese, E. M. 1988. Relationship between coyote group size and diet in southeastern Colorado. *Journal of Wildlife Management* 52:647-53.
- . 1989. Population dynamics of coyotes in southeastern Colorado. *Journal of Wildlife Management* 53:174-81.
- . 1995. Foraging ecology of coyotes in Yellowstone National Park. Ph.D. diss., University of Wisconsin, Madison.
- Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133:36-43.
- Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management* 52:640-46.
- 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. *Canadian Journal of Zoology* 74:784-97.
- . 1996b. Social and nutritional factors influencing the dispersal of resident coyotes. *Animal Behaviour* 52:1025-43.
- Gittleman, J. L. 1986. Carnivore life history patterns: Allometric, phylogenetic, and ecological associations. *American Naturalist* 127:744-71.
- Gittleman, J. L., and S. L. Pimm. 1991. Crying wolf in North America. *Nature* 351:524-25.
- Gottelli, D., and C. Sillero-Zubiri. 1992. The Ethiopian wolf: An endangered endemic canid. *Oryx* 26:205-14.
- Green, J. S., and J. T. Flinders. 1981. Diets of sympatric red foxes and coyotes in southeastern Idaho. *Great Basin Naturalist* 41:251-54.
- Hamlin, K. L., S. J. Riley, D. Pyrah, and R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48:489-99.

PRESCOTT COLLEGE LIBRARY

- Harris, C. E. 1983. Differential behavior of coyotes with regard to home range limits. Ph.D. diss., Utah State University, Logan.
- Harrison, D. J. 1992. Dispersal characteristics of juvenile coyotes in Maine. *Journal of Wildlife Management* 56:128-38.
- Harrison, D. J., J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. *Journal of Wildlife Management* 53:181-85.
- Harrison, D. J., and J. R. Gilbert. 1985. Denning ecology and movements of coyotes in Maine during pup rearing. *Journal of Mammalogy* 66:712-19.
- Hatier, K. G. 1995. Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming. M.S. thesis, Montana State University, Bozeman.
- Hersteinsson, P., A. Angerbjorn, K. Frajford, and A. Kaikusalo. 1989. The arctic fox in Fennoscandia and Iceland: Management problems. *Biological Conservation* 49:67-81.
- Hersteinsson, P., and D. W. Macdonald. 1982. Some comparisons between red and arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio tracking. *Symposia Zoological Society of London* 49:259-89.
- Hibler, S. J. 1977. Coyote movement patterns with emphasis on home range characteristics. M.S. thesis, Utah State University, Logan.
- Hixon, M. A., F. L. Carpenter, and D. C. Paton. 1983. Territory area, flower density, and time budgeting in hummingbirds: An experimental and theoretical analysis. *American Naturalist* 122:366-91.
- Hockman, J. G., and J. A. Chapman. 1983. Comparative feeding habits of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in Maryland. *American Midland Naturalist* 110:276-85.
- Houston, D. B. 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. *Journal of Applied Ecology* 15:653-61.
- Ingle, M. A. 1990. Ecology of red foxes and gray foxes and spatial relationships with coyotes in an agricultural region of Vermont. M.S. thesis, University of Vermont, Burlington.
- Jaksic, F. M., J. L. Yanez, and J. R. Rau. 1983. Trophic relations of the southernmost populations of *Dusicyon* in Chile. *Journal of Mammalogy* 64:697-700.
- Jimenez, J. E. 1993. Comparative ecology of *Dusicyon* foxes at the Chinchilla National Reserve in northeastern Chile. M.S. thesis, University of Florida, Gainesville.
- Johnson, W. E. 1992. Comparative ecology of two sympatric South American foxes, *Dusicyon griseus* and *Dusicyon culpaesus*. Ph.D. diss., Iowa State University, Ames.
- Johnson, W. E., and W. L. Franklin. 1994. The role of body size in the diets of sympatric grey and culpeo foxes. *Journal of Mammalogy* 75:163-74.
- Johnson, W. E., T. K. Fuller, and W. L. Franklin. 1996. Sympatry in canids: A review and assessment. Pp. 189-218 in J. L. Gittleman, ed., *Carnivore behavior, ecology, and evolution*, vol. 2. Cornell University Press, Ithaca.
- Keith, L. B., A. W. Todd, C. J. Brand, and R. S. Adamcik. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proceedings of the International Conference on Game Biology* 13:151-75.
- Kelly, B. 1991. Analysis of coyote scat and estimation of diet. M.S. thesis, University of Idaho, Moscow.
- Klett, S. 1987. Home ranges, movement patterns, habitat use, and interspecific interaction of red foxes and coyotes in northwest Louisiana. M.S. thesis, Southeast Louisiana University, Hammond.
- Knight, S. W. 1978. Dominance hierarchies of captive coyote litters. M.S. thesis, Utah State University, Logan.
- Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. *Journal of Wildlife Management* 36:369-82.
- Knowlton, F. F., and L. C. Stoddart. 1983. Coyote population mechanics: Another look. Pp. 93-111 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds., *Symposium on natural regulation of wildlife populations*. Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow.
- Knowlton, F. F., L. A. Windberg, and C. E. Wahlgren. 1986. Coyote vulnerability to several

Coyotes and Canid Coexistence

- management techniques. Pp. 165-76 in D. B. Fagre, ed., Proceedings of the seventh Great Plains wildlife damage control workshop, San Antonio. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Knudsen, J. J. 1976. Demographic analysis of a Utah-Idaho coyote population. M.S. thesis, Utah State University, Logan.
- Krefting, L. W. 1969. The rise and fall of the coyote on Isle Royale. *Naturalist* 20(4):24-31.
- Lamprecht, J. 1978. On diet, foraging behaviour and interspecific competition of jackals in the Serengeti National Park, East Africa. *Zeitschrift für Säugetierkunde* 43:210-33.
- Laundré, J. W. 1981. Home range use by coyotes in Idaho. *Animal Behaviour* 29:449-61.
- Laundré, J. W., and B. L. Keller. 1984. Home-range size of coyotes: A critical review. *Journal of Wildlife Management* 48:127-39.
- Lehman, N., A. Eisenhower, K. Hansen, L. D. Mech, R. O. Peterson, P. J. P. Gogan, and R. K. Wayne. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution* 45:104-19.
- Lewis, J. C., K. L. Sallee, and R. T. Golightly. 1993. Introduced red fox in California. California Resources Agency, Department of Fish and Game, Nongame Bird and Mammal Section Report 93-10, Sacramento.
- Litvaitis, J. A. 1992. Niche relations between coyotes and sympatric Carnivora. Pp. 73-85 in A. H. Boer, ed., Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, New Brunswick.
- Lott, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266-325.
- Major, J. T., and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *Journal of Wildlife Management* 51:606-16.
- Mares, M. A., T. E. Lacher, M. R. Willig, N. A. Bitar, R. Adams, A. Klinger, and D. Tazik. 1982. An experimental analysis of social spacing in *Tamias striatus*. *Ecology* 63:267-73.
- Mech, L. D. 1974. *Canis lupus*. *Mammalian Species* no. 37.
- . 1977. Wolf pack buffer zones as prey reservoirs. *Science* 198:320-21.
- Messier, F., and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. *Canadian Journal of Zoology* 60:1743-53.
- Messier, F., C. Barrette, and J. Huot. 1986. Coyote predation on a white-tailed deer population in southern Quebec. *Canadian Journal of Zoology* 64:1134-36.
- Mills, L. S., and F. F. Knowlton. 1991. Coyote space use in relation to prey abundance. *Canadian Journal of Zoology* 69:1516-21.
- Moehlman, P. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pp. 423-53 in J. F. Eisenberg and D. G. Kleiman, eds., Recent advances in the study of mammalian behavior. Special Publication no. 7, American Society of Mammalogists, Pittsburgh.
- . 1986. Ecology of cooperation in canids. Pp. 64-86 in D. I. Rubenstein and R. W. Wrangham, eds., Ecological aspects of social evolution: Birds and mammals. Princeton University Press, Princeton.
- Murie, A. 1940. Ecology of the coyote in the Yellowstone. National Park Service Fauna Series no. 4. U.S. Government Printing Office, Washington.
- . 1944. The wolves of Mount McKinley. National Park Service Fauna Series no. 5. U.S. Government Printing Office, Washington.
- Nel, J. A. J. 1984. Behavioural ecology of canids in the south-western Kalahari. *Koedoe* 1984:229-35.
- Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-68. *Journal of Wildlife Management* 40:389-99.
- Norris, P. W. 1881. Annual report of the superintendent of the Yellowstone National Park to the secretary of the interior for the year 1880. U.S. Government Printing Office, Washington.
- O'Farrell, T. P. 1984. Conservation of the endangered San Joaquin kit fox *Vulpes macrotis mutica* on the Naval Petroleum Reserves, California. *Acta Zoologica Fennica* 172:207-8.
- Packard, J. M., and L. D. Mech. 1980. Population regulation in wolves. Pp. 135-50 in M. N.

- Cohen, R. S. Malpass, and H. G. Klein, eds., Biosocial mechanisms of population regulation. Yale University Press, New Haven.
- Packer, C., D. Scheel, and A. E. Pusey. 1990. Why lions form groups: Food is not enough. *American Naturalist* 136:1-19.
- Paquet, P. 1989. Behavioral ecology of wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park, Manitoba. Ph.D. diss., University of Alberta, Edmonton.
- . 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park. *Journal of Mammalogy* 72:397-401.
- . 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park. *Journal of Mammalogy* 73:337-43.
- Peterson, R. O. 1996. Wolves as interspecific competitors in canid ecology. Pp. 315-23 in L. N. Carbyn, S. H. Fritts, and D. Seip, eds., *Wolves in a changing world*. Canadian Circumpolar Institute, University of Alberta, Edmonton.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences* 71:2141-45.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 52:137-54.
- 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 Service, Washington.
- Sargeant, A. B., and S. H. Allen. 1989. Observed interactions between coyotes and red foxes. *Journal of Mammalogy* 70:631-33.
- Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. *Journal of Wildlife Management* 51:285-93.
- Sayles, N. D. 1984. The effect of nutrition on maternal behavior among captive coyotes. M.S. thesis, Utah State University, Logan.
- Schamel, D., and D. M. Tracy. 1986. Encounters between arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*. *Canadian Field-Naturalist* 100:562-63.
- Schmitz, O. J., and D. M. Lavigne. 1987. Factors affecting body size in sympatric Ontario canids. *Journal of Mammalogy* 68:92-99.
- Schullery, P., and L. Whittlesey. 1992. The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882. Pp. 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 Service, Yellowstone National Park.
- Sheldon, J. W. 1992. *Wild dogs: The natural history of the nondomestic Canidae*. Academic Press, New York.
- Skinner, M. P. 1927. The predatory and fur bearing animals of the Yellowstone National Park. *Roosevelt Wildlife Bulletin* 4:163-281.
- Small, R. L. 1971. Interspecific competition among three species of Carnivora on the Spider Ranch, Yavapai Co., Arizona. M.S. thesis, University of Arizona, Tucson.
- Smits, C. M. M., B. G. Slough, and C. A. Yasui. 1989. Summer food habits of sympatric arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*, in the northern Yukon Territory. *Canadian Field-Naturalist* 103:363-67.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, M. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.
- Springer, J. T. 1982. Movement patterns of coyotes in south-central Washington. *Journal of Wildlife Management* 46:191-200.
- Steigers, W. D., and J. T. Flinders. 1980. Mortality and movements of mule deer in Washington. *Journal of Wildlife Management* 44:381-88.
- Stoel, P. F. 1976. Some coyote food habit patterns in the shrub-steppe of south-central Washington. M.S. thesis, Portland State University, Portland, Oregon.
- Theberge, J. B., and C. H. R. Wedeles. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. *Canadian Journal of Zoology* 67:1285-90.

Coyotes and Canid Coexistence

- Till, J. A., and F. F. Knowlton. 1983. Efficacy of denning in alleviating coyote depredations upon domestic sheep. *Journal of Wildlife Management* 47:1018-25.
- Todd, A. W., and L. B. Keith. 1976. Responses of coyotes to winter reductions in agricultural carrion. Wildlife Technical Bulletin no. 5, Alberta Department of Recreation, Parks, and Wildlife, Edmonton.
- Todd, A. W., L. B. Keith, and C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. *Journal of Wildlife Management* 45:629-40.
- Tzilkowski, W. M. 1980. Mortality patterns of radio-marked coyotes in Jackson Hole, Wyoming. Ph.D. diss., University of Massachusetts, Amherst.
- Van Valkenburgh, B., and R. K. Wayne. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* 75:1567-81.
- Voigt, D. R., and B. D. Earle. 1983. Avoidance of coyotes by red fox families. *Journal of Wildlife Management* 47:852-57.
- Waser, P. M. 1974. Spatial associations and social interactions in a "solitary" ungulate: The bushbuck *Tragelaphus scriptus* (Pallas). *Zeitschrift für Tierpsychologie* 37:24-37.
- Wayne, R. K., and S. M. Jenks. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature* 351:565-68.
- Weaver, J. L. 1977. Coyote-food base relationships in Jackson Hole, Wyoming. M.S. thesis, Utah State University, Logan.
- Wells, M. C., and M. Bekoff. 1982. Predation by wild coyotes: Behavioral and ecological analyses. *Journal of Mammalogy* 63:118-27.
- White, P. J., K. Ralls, and R. A. Garrott. 1994. Coyote-kit fox spatial interactions as revealed by telemetry. *Canadian Journal of Zoology* 72:1831-36.
- Windberg, L. A., H. L. Anderson, and R. M. Engeman. 1985. Survival of coyotes in southern Texas. *Journal of Wildlife Management* 49:301-7.
- Windberg, L. A., and F. F. Knowlton. 1988. Management implications of coyote spacing patterns in southern Texas. *Journal of Wildlife Management* 52:632-40.
- Wooding, J. B. 1984. Coyote food habits and the spatial relationship of coyotes and foxes in Mississippi and Alabama. M.S. thesis, Mississippi State University, State College.

MISSISSIPPI COLLEGE LIBRARY