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Coyote

Canis latrans

Marc Bekoff
Eric M. Gese

NOMENCLATURE

COMMON NAMES. Coyote, brush wolf, prairie wolf, Heul wolf, Steppenwolf, lobo, American jackal; the word *coyote* means "barking dog" and is taken from the Aztec word *coyotl*
SCIENTIFIC NAME. *Canis latrans*

The coyote is one of eight recognized species in the genus *Canis*. By the late Pliocene, the ancestral coyote, *Canis lepophagus*, was widespread in North America. The Eastern coyote, formerly referred to as the New England canid, appears to be a recent immigrant, having predominantly coyote ancestry with some introgression of wolf (*C. lupus*) and dog (*C. familiaris*) genes (Lawrence and Bossert 1969, 1975; Silver and Silver 1969; Bekoff et al. 1975; Hilton 1978; Wayne and Lehman 1992). Lehman et al. (1991) and Wayne and Lehman (1992) presented evidence that coyotes have interbred with wolves in areas where wolves are rare and conspecific mates may not be readily available.

Subspecies. There are 19 recognized subspecies of *C. latrans*. However, because of the mobility of coyotes, the integrity of individual subspecies and their taxonomic utility are questionable (Nowak 1978). In chronological order of being named, the subspecies are *C. l. latrans*, *C. l. ochropus*, *C. l. cagottis*, *C. l. frustror*, *C. l. lestes*, *C. l. mearnsi*, *C. l. microdon*, *C. l. peninsulae*, *C. l. vigilis*, *C. l. clepticus*, *C. l. impavidus*, *C. l. goldmani*, *C. l. texensis*, *C. l. jamesi*, *C. l. dickeyi*, *C. l. incolatus*, *C. l. hondurensis*, *C. l. thamnos*, and *C. l. umpquensis* (Jackson 1951).

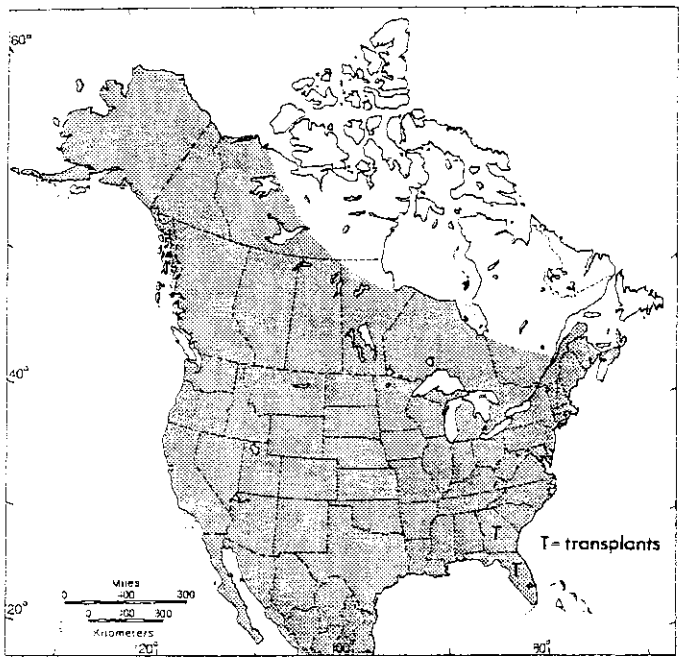

FIGURE 22.1. Distribution of the coyote (*Canis latrans*).

DISTRIBUTION

Coyotes are Nearctic canids. They occupy many diverse habitats between about 10°N latitude (Costa Rica) and 70°N latitude (northern Alaska). They are found throughout the continental United States and in many areas of Canada (Fig. 22.1). In some southeastern states, such as Florida (Cunningham and Dunford 1970) and Georgia (Fisher 1975), and several eastern states, it appears that coyotes were transplanted, introduced, or liberated by humans (Schultz 1955; Hill et al. 1987). See Moore and Parker (1992) for the history of coyote expansion and changes in distribution. With its ability to adapt to an environment modified by humans, coyotes are now observed in large cities (Shargo 1988; Quinn 1997a, 1997b; Grinder and Krausman 1998; Finkel 1999).

DESCRIPTION

Coyotes are often confused with other canids, such as gray wolves, red wolves (*C. rufus*), and domestic dogs. Coyotes can successfully interbreed and produce fertile hybrids with all these species (Dice 1942; Kennelly and Roberts 1969; Kolenosky 1971). However, coyotes can usually be differentiated (although overlap and hybridization can occur) using serologic parameters, dental characteristics, cranial measurements, neuroanatomical features, diameter of the nose pad, diameter of the hind foot pad, ear length, track size, stride length, pelage, behavior, and genetics (for reviews, see Lawrence and Bossert 1967; Bekoff 1977a; Elder and Hayden 1977). For example, coyotes are typically smaller than gray wolves (Table 22.1), thus the nose pad (about 25 mm in diameter) and hind foot pads (less than 32 mm) are correspondingly smaller.

Coyotes may be differentiated from dogs using the ratio of palatal width (distance between the inner margins of the alveoli of the upper first molars) to the length of the upper molar toothrow (from the anterior margin of the alveolus of the first premolar to the posterior margin of the last molar alveolus) (Howard 1949). If the toothrow is 3.1 times the palatal width, the specimen is a coyote; if the ratio is less than 2.7, the specimen is a dog (this method is about 95% reliable).

The coyote has a relatively larger braincase than *C. lupus* (Mech 1974). The coyote brain is anatomically different from that of gray wolves (Radinsky 1973; Atkins 1978). The wolf has a dimple in the middle of the coronal gyrus, whereas the coyote does not (see also Atkins and Dillon 1971). There is no overlap when comparing large coyotes to small wolves in zygomatic breadth (greatest distance across zygomata), greatest length of the skull, or bite ratio (width across the outer edges of the alveoli of the anterior lobes of the upper carnassials divided by the length of the upper molar toothrow) (Paradiso and Nowak 1971). *C. latrans* is usually smaller than *C. rufus* and there is almost no overlap between them in greatest length of the skull. Red wolves also have a more pronounced sagittal crest than coyotes. Multivariate techniques have clearly shown that coyotes, wolves, and dogs can be differentiated anatomically (Lawrence and Bossert 1967; Elder and Hayden 1977) and behaviorally (Bekoff et al. 1975; Bekoff 1978) and

TABLE 22.1. Representative mean coyote weights from a variety of locales

Source	Adults (kg)		Juveniles (kg)		State/Province
	Males	Females	Males	Females	
Gier 1968	14.1	11.8	—	—	Kansas
Hawthorne 1971	11.2	9.8	—	—	NE California
Richens and Hugie 1974	15.8	13.7	—	—	Maine
Andrews and Boggess 1978	13.4	11.4	—	—	Iowa
Berg and Chesness 1978	12–13	11–12	10–11	10	Minnesota
Boggess and Henderson 1978	13.1	11.0	—	—	Kansas
Bowen 1978	12.1	11.5	—	—	Alberta
Litvaitis 1978	14.7	12.1	—	—	Oklahoma
Murray and Boutin 1991	10.3	8.0	—	—	Yukon
Thurber and Peterson 1991	12.9	11.1	—	—	Alaska
Windberg et al. 1991	10.6–11.4	9.1–9.6	10.0–10.8	8.6–8.9	Texas
Poulle et al. 1995	12.5–16.0	11.0–14.2	—	—	Quebec
Windberg 1995	10.9–11.0	—	8.8–9.2	8.0–8.4	Texas

provide for more rigorous analyses than do univariate methods. Further refinement of genetic techniques will also assist in differentiation of the canids (e.g., Lehman et al. 1991; Wilson et al. 2000).

Size and Weight. Coyotes are about 1–1.5 m in body length; the tail is about 400 mm long. Size varies with geographic locale and subspecies (Jackson 1951; Hall and Kelson 1959). Adult males are usually heavier and larger than adult females (Table 22.1). Temporal changes in coyote morphology may be occurring in some parts of North America (Schmitz and Lavigne 1987; Thurber and Peterson 1991), but see Larivière and Crête (1993) and Peterson and Thurber (1993) for reviews and comments.

Pelage. The banded nature of coyote hair is responsible for the appearance of the blended color, gray mixed with a reddish tint. Coyotes show great variation in color, ranging from almost pure gray to rufous. Melanistic coyotes are rare (Young 1951; Van Wormer 1964; Gipson 1976; Mahan 1978). Texture and color of the fur also vary geographically. In northern subspecies, the hair is longer and coarser. In desert habitats, coyotes tend to be fulvous, whereas those at higher latitudes are more gray and black (Jackson 1951). The belly and throat are paler than the rest of the body. Course guard hairs are about 50–90 mm long; in the mane, they tend to be 80–110 mm. The fine underfur (up to 50 mm long) has coronal-shaped cuticular scales (Adorjan and Kolenosky 1969; Ogle and Farris 1973). The summer coat is shorter than the winter coat. Coyote hair may be differentiated from hair of dogs and red foxes (*Vulpes vulpes*) by the number, order, and color of the bands, the cross-sectional translucence and shape, and the coronal scale pattern (Hilton and Kutscha 1978). Coyote hairs typically are coarser, longer, larger in diameter, and rougher and stiffer.

The coyote's fur is similar in insulative value to that of the gray wolf (Ogle and Farris 1973). The critical temperature of *C. latrans* is −10°C (Shield 1972). When wearing the shorter summer coat, there is a decrease of about 87% in thermal conductivity (Ogle and Farris 1973). There is usually one main molt between late spring and autumn. About 50 mm down from the base of the tail there is an oval tail gland (Hildebrand 1952).

Skull and Dentition. Among adult coyotes, males show greater development of the sagittal crest than females. The dental formula is I 3/3, C 1/1, P 4/4, M 2/3 (Fig. 22.2). The skull of a mature male is about 180–205 mm long from the tip of the premaxilla to the posterior rim of the coronal crest (Gier 1968) and weighs between 170 and 210 g.

PHYSIOLOGY

Central Nervous System. Although the cerebrum and cerebellum share many common features with other canids, there are some interspecific differences (for reviews see Atkins and Dillon 1971; Atkins 1978). With respect to cerebellar morphology, coyotes may be distinguished from all other canids as follows: The anterior lobe is more than one half the total width, the parafloccular process is relatively prominent, the vermian lobule reaches its greatest size, there are fewer and larger posterior hemispheric folia, the posterior ventral parafloccular limb is reduced in size, and there is a broad vermian twist (Atkins 1978). The remainder of the central nervous system, the brain stem and spinal cord, is similar to that of the domestic dog.

Adrenals. Coyote adrenals are similar in structure to those of most other canids (Heinrich 1972). In males and females, the left adrenal is heavier than the right, and the adrenals of females tend to be heavier than those of males.

Audition and Vision. The region of maximal sensitivity to auditory stimuli is 100–30,000 Hz with a limit of approximately 80 kHz (Petersen et al. 1969). The retina is duplex and has a preponderance of rods. The absolute scotopic (rod) threshold is about 1.4 ft-candles and the adaptation curve shows distinct rod–cone breaks (Horn and Lehner 1975).

REPRODUCTION

Genetics and Hybridization. The coyote has 38 pairs of chromosomes (Wurster and Benirschke 1968). The autosomes are acrocentric or telocentric and the sex chromosomes are submetacentric (Mech 1974). Fertile hybrids have been produced by matings of coyotes with domestic dogs (Dice 1942; Young 1951; Kennelly and Roberts 1969; Silver and Silver 1969; Mengel 1971), red and gray wolves (Young 1951; Kolenosky 1971; Paradiso and Nowak 1971; Riley and McBride 1975), and golden jackals (*C. aureus;* Seitz 1965). Coyote–dog hybrids exhibit decreased fecundity (Mengel 1971; Gipson et al. 1975). Hybridization between coyotes and red wolves is becoming problematic for red wolf recovery in the southeast United States.

Anatomy and Physiology. There are no detailed reports of the gross or microscopic anatomy of coyote reproductive systems. Patterns of reproductive hormones and reproductive behaviors in coyotes have been described (Bekoff and Diamond 1976; Hodges 1990; Parrish 1994). With the exception of the seasonality of breeding and associated changes in reproductive anatomy and physiology, there appear to be only minor differences, if any, between coyotes and domestic dogs (Kennelly 1978). Berg and Chesness (1978) found no correlation between carcass weight and ovarian weight ($n = 105, r = .218, p > .05$).

Kennelly (1972, 1978) documented spermatogenesis and the estrous cycle. Proestrus lasts about 2–3 months and estrus up to 10 days, depending on locale (Hamlett 1939; Kennelly 1978). Copulation ends with the copulatory "tie," during which time (up to 25 min) the male's penis is locked in the female's vagina (Grandage 1972). Juvenile males and females are able to breed (see below), although juvenile females may ovulate less than adult females.

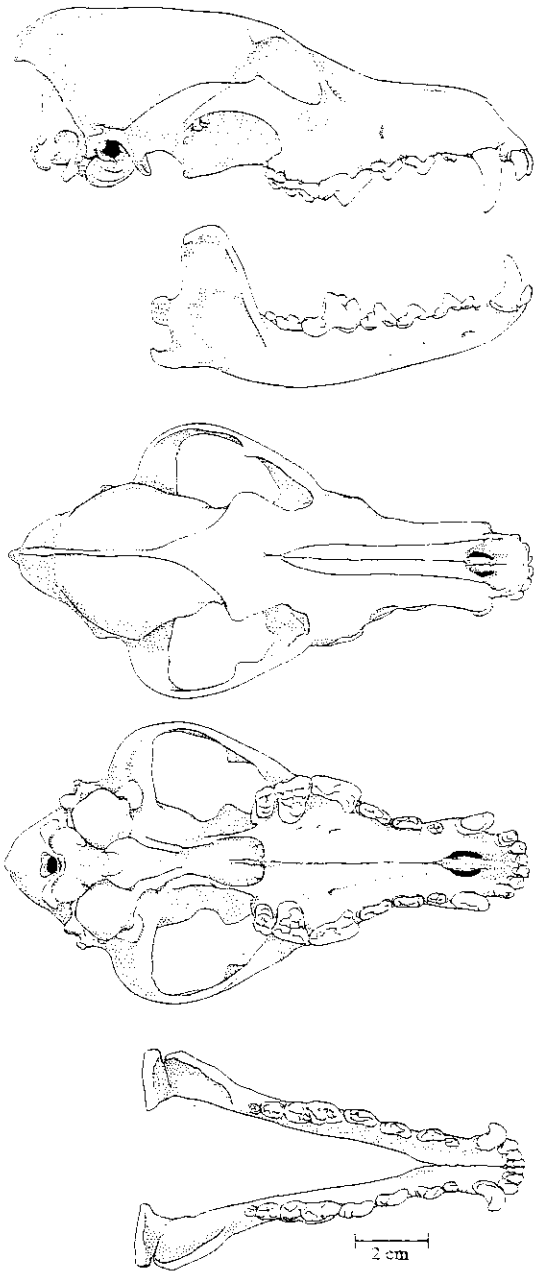

FIGURE 22.2. Skull of the coyote (*Canis latrans*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

Males and females show annual cyclic changes in reproductive anatomy and physiology (Kennelly 1978). Females are seasonally monestrus, showing one period of "heat" per year, usually during January and March, depending on geographic locale (Hamlett 1939; Gier 1968; Kennelly 1978).

Pair Bonding. The dynamics of heterosexual pair bonding are not known for wild coyotes in any detail. Data on captive individuals do not appear to differ significantly from those for wild coyotes. Courtship may begin as long as 2–3 months before successful copulation (Bekoff and Diamond 1976). Associated changes in behavior have been described, especially increases in scent marking and howling observed at the beginning of the breeding season (Bekoff and Diamond 1976; Wells and Bekoff 1981; Hodges 1990; Gese and Ruff 1997, 1998). During early stages of courtship, the male becomes increasingly attracted to the female's urine and feces. When the female is ready to copulate, she will tolerate mounting attempts by the male and will flag her tail to one side. When tying, the male steps over the female's back and the couple remain locked at 180° for up to 25 min. The same pair may breed from year to year, but not necessarily for life. Adult coyotes may maintain pair bonds and whelp or sire pups even when 10–12 years of age (Gese 1990).

Pregnancy Rate, Gestation, and Litter Size. The percentage of females that breed in a given year varies with local conditions (Gier 1968; Knowlton 1972; Gipson et al. 1975; Gese et al. 1989a; Knowlton and Gese 1995). Food supply is usually the prime factor; in good years, more females, especially yearlings, breed (Gier 1968; Knowlton and Gese 1995). Usually, about 60–90% of adult females and 0–70% of female yearlings will produce litters (Knowlton 1972; Gese et al. 1989a; Knowlton et al. 1999). The greatest annual variation in the number of breeding females is related to the number of juveniles that become sexually mature (Knowlton 1972; Kennelly 1978; Gese et al. 1989a). Adults may show more placental scars than yearlings; however, Nellis and Keith (1976) reported that the difference was not statistically significant. Gier (1975) estimated that the number of young born was about 80% of the ova shed, and Knowlton (1972) estimated that about 87% of implants were represented by viable young. Gipson et al. (1975) reported the mean number of ova per breeding female was 6.2, with 4.5 (73%) becoming implanted. Hamlett (1939) and Asdell (1964) reported that 85–92% of embryos develop into viable young.

Gestation lasts approximately 63 days. Average litter size is 6, but it is known that litter size is affected by population density and food availability the previous winter (Knowlton 1972; Gese et al. 1996a, 1996b; Knowlton et al. 1999). Knowlton (1972) reported average litter sizes of 4.3 at high population densities and 6.9 at low densities. Gier (1968) reported the effects of food on litter size. During years of high rodent density, mean litter size is higher (5.8–6.2) than in years of reduced densities of rodents (4.4–5.1). In northern climes, coyote litter size changes in response to cycles of snowshoe hares (*Lepus americanus*) (Todd et al. 1981; Todd and Keith 1983; O'Donoghue et al. 1997). Gese et al. (1996a) found an increase in coyote litter size after cold, snowy winters in Yellowstone National Park. Winters with harsh temperatures and deep snow increased the number of ungulate carcasses (because of coyote predation and weather) available to ovulating females. The sex ratio of litters is generally 1:1, though it may be skewed toward females in areas of high exploitation (Knowlton 1972; Berg and Chesness 1978; Kleiman and Brady 1978; Gese et al. 1989a).

Development. Young are born blind and helpless in a den. Birth weight is about 240–275 g and the length of the body from the tip of the head to the base of the tail is about 160 mm (Gier 1968; Bekoff and Jamieson 1975). Eyes open at about 14 days. Teeth erupt on the average as follows: upper canines, day 14; lower canines and upper incisors, day 15; and lower incisors, day 16 (Bekoff and Jamieson 1975). The young are able to urinate and defecate on their own by 2–3 weeks. They emerge from the den at about 3 weeks. Young are cared for by the mother and by other "helpers," usually siblings from a previous year (Bekoff and Wells 1980; Hatier 1995). Food provisioning of the female may occur during the nursing period (Hatier 1995). The alpha male and other associates will also help to rear the young by providing food as the young grow older (Hatier 1995). Young are weaned at about 5–7 weeks (Snow 1967). They begin to eat solid food at about 3 weeks, when the caregivers regurgitate semisolid food. Between birth and week 8, average weight increase is about 310 g/week. The pups reach adult weight at about 9 months.

ECOLOGY

More is known about the ecology of coyotes than perhaps any other carnivore (Bekoff 2001a). Coyotes occupy a variety of habitats, including grasslands, deserts, and mountains. They do not compete well with larger carnivores and may be killed by them or avoid areas and habitats occupied by these species. Studies have documented direct and indirect competition with larger carnivores, such as wolves (Mech

1966, 1974; Krefting 1969; Fuller and Keith 1981; Thurber et al. 1992; Peterson 1995; Arjo and Pletscher 1999; Crabtree and Sheldon 1999) and cougars, *Puma concolor* (Young 1951; Boyd and O'Gara 1985; Koehler and Hornocker 1991; Murphy 1998). Arjo and Pletscher (1999) documented behavioral changes in coyotes after several years of increased wolf abundance in northwestern Montana. Paquet (1991, 1992) reported that coyotes did not spatially avoid wolves, but actually followed their trails and scavenged wolf-killed ungulates.

Interspecific killing appears to be common in carnivore communities (Peterson 1995; Palomares and Caro 1999). In Yellowstone National Park, Crabtree and Sheldon (1999) reported that wolves killing coyotes during the winters of 1997 and 1998 reduced coyote numbers; average pack size decreased from 6 coyotes to 4 (a 33% decline). However, Gese et al. (1996a, 1996b) documented similar annual variations in coyote pack sizes in the same area in the absence of wolves. Average pack size changed from 4.6 to 6.8 coyotes during three winters (1990–93) several years before wolf reintroduction, an increase of 32%. Thus, annual variation in coyote pack size and population size attributed to wolf reintroduction should be viewed in the context of baseline population data that documented these same fluctuations had occurred before wolf reintroduction. Changes in the abundance of food resources, mainly cyclic lagomorph populations, causes even greater annual variations (3–10 times) in coyote populations than populations exposed to wolves (Todd et al. 1981; Knowlton and Stoddart 1992; O'Donoghue et al. 1997). Direct predation and competition for food and space with wolves may limit coyote numbers in some areas and under certain environmental conditions (Peterson 1995; Arjo and Pletscher 1999).

Coyotes may not tolerate red foxes in some areas (Voigt and Earle 1983; Major and Sherburne 1987; Sargeant et al. 1987; Harrison et al. 1989; Sargeant and Allen 1989), but appear to be more tolerant of red foxes when food is abundant (Gese et al. 1996d). Coyotes also will kill many of the small canids, particularly swift (*Vulpes velox*), kit (*V. macrotis*), and gray foxes (*Urocyon cinereoargenteus*). Coexistence between coyotes and these small canids is typically mediated by resource partitioning (Ralls and White 1995; White et al. 1995; Cypher and Spencer 1998; Kitchen et al. 1999). Bobcats (*Lynx rufus*) also may not be well tolerated by coyotes (Young 1951), but Major and Sherburne (1987) found no evidence of interference competition between bobcats and coyotes. Soulé et al. (1988) and Crooks and Soulé (1999) reported that coyotes in southern California apparently control the abundance and distribution of smaller predators. In the absence of coyotes, these mesopredators (i.e., foxes and feral cats) increase in density. They prey on native bird species and negatively impact the avifaunal community. Henke and Bryant (1999) documented that coyotes were considered a keystone predator shaping faunal community structure in west Texas.

Population Regulation. Population demographics of coyotes have been studied throughout North America (e.g., Gier 1968; Knowlton 1972; Todd and Keith 1983; Windberg 1995). They exhibit a land-tenure system of exclusive territories (Camenzind 1978; Bowen 1981, 1982; Messier and Barrette 1982; Windberg and Knowlton 1988; Knowlton and Gese 1995), and within resident packs, they display a dominance hierarchy similar to that of wolves (Camenzind 1978; Bowen 1978; Bekoff and Wells 1986; Gese et al. 1996a). The social organization and land-tenure system mediate the regulation of coyote numbers as packs space themselves across the landscape in relation to available food and habitat (Knowlton and Stoddart 1983; Bekoff and Wells 1986; Gese et al. 1988a; Knowlton and Gese 1995; Knowlton et al. 1999). The social hierarchy and dominance structure among members of resident packs also influence accessibility to food resources (Gese et al. 1996a, 1996b). Older, experienced pack members are more successful hunters of large prey (Gese and Grothe 1995), have greater access to ungulate carcasses (Gese et al. 1996b), and are more proficient hunters of small mammals (Gese et al. 1996c). Transient or nomadic coyotes also exist across the landscape (Camenzind 1978; Bowen 1982; Bekoff and Wells 1986; Gese et al. 1988a) and may move into territories whenever vacancies occur.

TABLE 22.2. Coyote densities in different geographic areas and seasons

Source	Location	Density (individuals/km^2)
Gier 1968	Kansas	0.8[a]
Knowlton 1972	Texas	0.9[a]; 1.5–2.3[b]
Chesness and Bremicker 1974	Minnesota	0.2–0.4[a]
Nellis and Keith 1976	Alberta	0.1–0.6[c]
Bowen 1978	Alberta	0.46[a]; 0.35[d]
Todd et al. 1981	Alberta	0.08–0.44[e]
Pyrah 1984	Montana	0.15[e]; 0.39[f]
Andelt 1985	Texas	0.9[g]
Gese et al. 1989a	Colorado	0.26–0.33[g]
Babb and Kennedy 1989	Tennessee	0.35[g]
O'Donoghue et al. 1997	Yukon	0.01–0.09[e]
Henke and Bryant 1999	Texas	0.12–0.14[g]

[a]Postwhelping.
[b]Fall.
[c]Winter.
[d]Late winter.
[e]Spring.
[f]Summer.
[g]Prewhelping.

Coyote density varies geographically and seasonally (Table 22.2) in response to changing food resources. Available food, whether rabbits, rodents, or ungulates, is the major factor regulating coyote populations (Gier 1968; Clark 1972; Knowlton and Stoddart 1992; O'Donoghue et al. 1997). Nutritional pressures for limited food resources are mediated through social dominance and territoriality (Knight 1978; Davison 1980; Knowlton and Stoddart 1983; Gese et al. 1989a; Knowlton and Gese 1995; Windberg 1995; Knowlton et al. 1999). Food abundance regulates coyote numbers by influencing pack size, reproductive rates, survival, dispersal, and space-use patterns (Gier 1968; Knowlton 1972; Todd et al. 1981; Todd and Keith 1983; Todd 1985; Bekoff and Wells 1986; Mills and Knowlton 1991; Harrison 1992; Windberg 1995; Gese et al. 1996a; O'Donoghue et al. 1997; Knowlton et al. 1999). In areas with hard winters, when carrion biomass is low, coyote pack sizes remain small and the core social unit subsists on small mammals (Gese et al. 1996a, 1996b). In contrast, during winters when carrion biomass is greater, more coyotes remain in their social groups and pack size increases (Gese et al. 1996a, 1996b). In addition, dominant individuals in resident packs have greater access to carcasses and are thereby less likely to disperse (Gese et al. 1996a, 1996b). Thus, dominance plays an important role in regulating coyote numbers. Knowlton et al. (1999) reported that the acquisition of a territory is also important because resident coyotes are more apt to survive, have more breeding opportunities, and are more likely to have access to carcasses in winter than are transient individuals (Andelt 1985; Bekoff and Wells 1986; Gese et al. 1989a, 1996a, 1996b).

Within resident coyote packs, size and structure change seasonally (Knowlton 1972; Davison 1980; Bekoff and Wells 1986; Gese et al. 1996a). Pack size increases during the whelping season (April), followed by a gradual decline as pups die or disperse and associated pack members disperse during winter as food resources become more limited (Knowlton 1972; Davison 1980; Gese et al. 1996a; Knowlton et al. 1999). If more food resources are available over winter, pack size may increase (Gese et al. 1996a, 1996b).

Effects of Exploitation. There have been few studies of unexploited coyote populations (Andelt 1985; Bekoff and Wells 1986; Crabtree 1988; Gese et al. 1989a, 1996a; Windberg 1995). These populations generally differ from exploited populations by having an older age structure, higher survival rates, lower reproductive rates, larger pack size, and lower recruitment into the adult population (Andelt 1985; Windberg et al. 1985; Gese et al. 1989a, 1996a, 1996b; Windberg 1995; Knowlton et al. 1999). Under high levels of exploitation, coyote populations

usually have a younger age structure, lower survival, increased numbers of yearlings reproducing, increased litter size, and relatively small packs (Gier 1968; Knowlton 1972; Berg and Chesness 1978; Davison 1980; Andelt 1987; Knowlton et al. 1999). Litter size may increase due to reduced coyote density, likely in response to reduced competition for food (Andelt 1987, 1996) or breeding among younger females (Knowlton et al. 1999).

Life Expectancy. Coyotes in captivity may live as long as 18 years (Young 1951), but in wild populations, life expectancy is considerably shorter. Maximum ages reported for wild coyotes are 13.5 (Nellis and Keith 1976), 14.5 (Knowlton 1972), and 15.5 years (Gese 1990).

Dens. Coyotes den in a variety of places, including brush-covered slopes, steep banks, under rock ledges, thickets, and hollow logs. Dens of other animals, including badgers (*Taxidea taxus*), are frequently used. Dens may have more than one entrance (Harrison and Gilbert 1985) and often there are many interconnecting tunnels. Dens may be oriented to the south to maximize solar radiation (Gier 1968; Hallett 1977; Harrison and Gilbert 1985). The same den may be used from year to year. Den sharing occurs only rarely (Nellis and Keith 1976; Camenzind 1978). Movement of pups among dens is very common (Harrison and Gilbert 1985). Reasons for these moves are not known, but disturbance (Harrison and Gilbert 1985) and possibly infestation by parasites may be factors. Most moves are relatively short; however, moves of >2 km are common (Harrison and Gilbert 1985). Van Wormer (1964) reported that a male coyote moved four pups, individually, a distance of 8.0 km. The den and pup-rearing activities are the focal point for coyote families for several months until pups are large and mobile (Andelt et al. 1979; Harrison and Gilbert 1985; Bekoff and Wells 1986; Hatier 1995).

Activity and Movements. Coyotes are active throughout the day, but tend to be more active during the early morning and around sunset (Woodruff and Keller 1982; Andelt 1985; Gese et al. 1989b). Gipson and Sealander (1972) showed a principal activity peak at sunset and a minor peak at daybreak in Arkansas. Activity patterns may change seasonally (Holzman et al. 1992a) or in response to human disturbance and persecution (Gese et al. 1989b; Kitchen et al. 2000a). Seasonal activity patterns also are obvious, especially during winter months, when there is a change in food base (Bekoff and Wells 1986; Gese et al. 1996a). For example, coyotes living in northern climates rest more during winter months, when they are dependent primarily on ungulate carrion for food, than during other seasons, when they feed mainly on small rodents (Bekoff and Wells 1981; Gese et al. 1996a). Hunting attempts also decrease during winter months, when rodents are relatively inaccessible because of snow-covered ground, one of the major rodent food items (Uinta ground squirrels, *Spermophilus armatus*) are hibernating, and ungulate vulnerability to predation increases with snow accumulation (Bekoff and Wells 1986; Gese and Grothe 1995; Gese et al. 1996a). In contrast, Shivik et al. (1997) reported a change in coyote activity levels during winter that was not dependent on a change in prey base. They theorized that the reduced activity levels helped reduce energy expenditures in an area with a limited food base. Coyotes living in packs rest more and travel less during winter months than do coyotes living as mated pairs or alone (Bekoff and Wells 1981, 1986; but see Gese et al. 1996a). Larger energy savings have been shown for a pregnant female living in a pack than for a female living only with her mate (Bekoff and Wells 1981). However, it is unknown whether females living in packs are better off reproductively because of the energy saved during pregnancy.

Coyotes, similar to wolves, are typically territorial, and primarily remain within their territory. However, they also may make extraterritorial movements into neighboring territories. Dispersal from the natal site may be into a vacant or occupied territory in an adjacent area or they may disperse long distances (Harrison et al. 1991). In general, it is the pups or subordinate yearlings that typically disperse (Knowlton 1972; Nellis and Keith 1976; Berg and Chesness 1978; Gese et al. 1989a, 1996a). Dispersal appears to be voluntary as social and nutritional pressures intensify during the winter and availability and access to food becomes more limited (Gese et al. 1996a; Bekoff 2001a). There are no consistent sex differences in dispersal distance (Gese et al. 1989a; Harrison et al. 1991), although in one study, female pups moved farther than male pups (Nellis and Keith 1976). Dispersal by juveniles usually occurs during autumn and early winter, though some individuals do not disperse during the first year and remain to provide care for future siblings (Hatier 1995; Gese et al. 1996a). Dispersal direction appears to be random, and pups will move 80–160 km (Bowen 1982; Gese et al. 1989a), with a record dispersal of 544 km (Carbyn and Paquet 1986). Berg and Chesness (1978) reported mean dispersal distances of 48 km, which occurred at a mean rate of about 11 km/week. Forays or exploratory movements also may occur before dispersal (Harrison et al. 1991). Increased mortality may be associated with dispersal as animals move into unfamiliar areas and low-security habitats (Tzilkowski 1980; Pyrah 1984; Bekoff and Wells 1986; Gese et al. 1989a). Observations of coyote dispersal are summarized in Table 22.3.

Home Range and Territory. Home range size of coyotes has been studied throughout their range. Home range size varies geographically and seasonally (Gipson and Sealander 1972; Bekoff and Wells 1980; Laundré and Keller 1984) and within a population (Springer 1977; Bowen 1982; Gese et al. 1988a) (Table 22.4). Variation in home range size among resident coyotes within a population depends on energetic requirements, season, sex, physiographic makeup, habitat, and food distribution (Laundré and Keller 1984; Gese et al. 1988a). Home range size also is influenced by social organization. Transient individuals

TABLE 22.3. Average distances of coyote dispersal movements from established home ranges

	Adults (km)		Juveniles (km)		
Source	Males	Females	Males	Females	Both Sexes
Robinson and Cummings 1951	12.6	17.8	—	—	16.8
Young 1951	36.2	—	—	—	—
Young 1951	45.3	40.0	—	—	—
Robinson and Grand 1958	45.6	34.2	—	—	40.6
Hawthorne 1971	6.4	7.6	5.2	6.4	—
Gipson and Sealander 1972	20.5	8.2	—	7.4	—
Nellis and Keith 1976	5.5	6.6	28.2 (5.8)[a]	31.5 (23.5)[b]	—
Andrews and Boggess 1978	30.2	31.2[c]	—	—	—
Bowen 1982	19.3	24.6	17.1	51.4	—
Gese et al. 1989a	—	—	—	—	59.0
Harrison 1992	—	—	113	94	—

[a]Male pups.
[b]Female pups.
[c]Excludes data for one female that moved a record distance of 323.2 km.

TABLE 22.4. Mean coyote home range sizes from some representative studies

Study	Adults (km^2)		Juveniles and Pups (km^2)		State/Province
	Males	Females	Males	Females	
Gipson and Sealander 1972	32.8	13.1	—	11.8	Arkansas
Chesness and Bremicker 1974	41.9	10.0	—	—	Minnesota
Berg and Chesness 1978	68.0	16.0	—	—	Minnesota
Hibler 1977	17.8	20.2	—	—	Utah
Litvaitis 1978	15.0	27.9	—	21.3	Oklahoma
Bowen 1982	13.9[a]	10.3[a]	—	—	Alberta
	14.9[b]	16.3[b]	—	—	
Pyrah 1984	9.7	7.8	—	—	Montana
Andelt 1985	2.7[c]	2.6[c]	—	—	Texas
	3.0[d]	2.1[d]	—	—	
	2.8–3.3[e]	2.3–2.5[e]	—	—	
	3.5[f]	2.7[f]	—	—	
Gese et al. 1988a	8.5[c]	8.7[c]	—	—	Colorado
	10.0[d]	7.7[d]	—	—	
	11.9[e]	9.1[e]	—	—	
	9.3[f]	8.8[f]	—	—	
Windberg and Knowlton 1988	—	2.8[g]	—	—	Texas
	—	2.3[h]	—	—	
Atkinson and Shackleton 1991	7.7	17.0	—	—	British Columbia
Person and Hirth 1991	10.4[a]	6.6[a]	—	—	Vermont
	18.8[b]	11.8[b]	—	—	
Holzman et al. 1992a	6.0[c]	18.9[c]	2.6[c]	4.5[c]	Georgia
	3.3[d]	9.8[d]	2.2[d]	2.4[d]	
	4.3[e]	21.9[e]	2.9[e]	4.6[e]	
	6.5[f]	24.8[f]	5.1[f]	6.5[f]	
Windberg et al. 1997a	5.9	5.4	—	—	New Mexico

[a]Summer.
[b]Winter.
[c]Breeding.
[d]Gestation.
[e]Pup rearing.
[f]Dispersal.
[g]Fall.
[h]Spring.

range over large areas, whereas residents occupy distinct territories (Bowen 1982; Bekoff and Wells 1986; Gese et al. 1988a). Coyotes living in packs who defend ungulate carrion during the winter have much smaller, compressed home ranges than coyotes living in pairs or alone (Bekoff and Wells 1980). Coyotes actively defend well-defined territorial boundaries using direct confrontation and indirect means involving scent marking and howling (Camenzind 1978; Bekoff and Wells 1980, 1986; Wells and Bekoff 1981; Gese and Ruff 1997, 1998; Gese 2001). Typically, only pack members maintain and defend territories; solitary individuals do not (Bekoff and Wells 1980; Gese and Ruff 1997, 1998; Gese 2001). Fidelity to the home range area is very high among resident animals, may persist for many years (Kitchen et al. 2000b), and may be passed to successive generations. Shifts in territorial boundaries may occur in response to loss of one or both of the alpha pair (Camenzind 1978; Gese 1998).

FEEDING HABITS

Coyotes are opportunistic, generalist predators and eat a variety of food items in relation to changes in availability (Van Vuren and Thompson 1982; Todd and Keith 1983; Andelt et al. 1987; Windberg and Mitchell 1990). They will consume food items ranging in size from fruit and insects to large ungulates and livestock (Fig. 22.3). MacCracken and Hansen (1987) suggested that coyotes may select prey as predicted by optimal foraging models, but see Boutin and Cluff (1989) and MacCracken (1989) for review and comments.

Gipson (1974) found regional and seasonal differences in feeding habits of coyotes living in Arkansas. The most common food items from 168 coyote stomachs were poultry (34%), persimmons (23%), insects (11%), rodents (9%), songbirds (8%), cattle (7%), rabbits (7%), deer (5%), woodchucks (4%), goats (4%), and watermelon (4%). Korschgen (1973), in an analysis of coyote feeding habits in Missouri, also found seasonal differences. For example, rabbits were found in 57% of coyote stomachs in winter versus 14.8% in spring. Carrion was found in 15.6% of stomachs in winter versus 37.0% in spring. Livestock and wild ungulates often may be found in coyote stomachs and scats as carrion (Murie 1935, 1951; Ozoga and Harger 1966; Korschgen 1973; Weaver

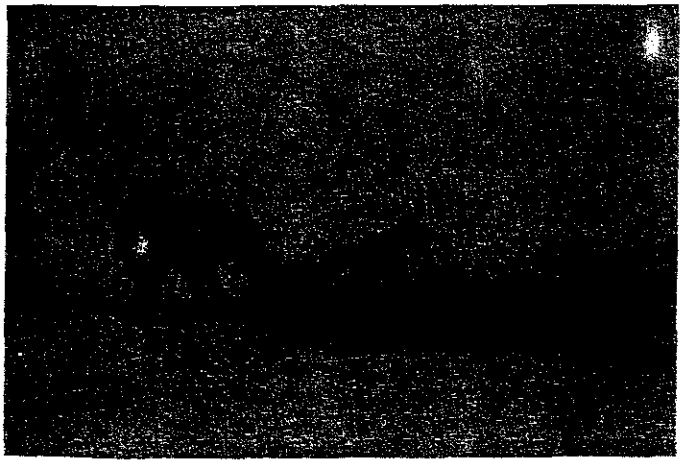

FIGURE 22.3. Coyote feeding on elk calf carcass, Yellowstone National Park, Wyoming. SOURCE: Photo by E. Gese.

1977; Bekoff and Wells 1980), but actual predation on large ungulates, both native and domestic, does occur (Gier 1968; Andelt 1987; Gese and Grothe 1995). In Wyoming, the percentage of coyote stomachs containing ungulate meat from scavenging carrion may increase as much as threefold in winter compared to summer (Weaver 1977, 1979; Houston 1978). Carrion availability during winter plays a large role in coyote foraging and population ecology in northern regions (Weaver 1979; Todd 1985; Gese et al. 1996a, 1996b). Reproductive status may also influence coyote feeding habits. Coyotes that are provisioning pups may switch to larger, more energetically "profitable" prey items as compared to nonreproductive coyotes (Till and Knowlton 1983; Harrison and Harrison 1984; Bromley 2000). Coyotes in suburban areas are equally adept at exploiting human-made food resources and will readily consume dog food or other human-related items (Shargo 1988; Atkinson and Shackleton 1991; McClure et al. 1995). As a caveat for food habit analysis, whenever scat analysis data are used to determine feeding habits, the inherent problems of prey digestibility and recovery of food items in relation to actual prey consumption can confound results and should be considered (Weaver and Hoffman 1979; Kelly and Garton 1997).

BEHAVIOR

Direct observation of coyote behavior in the wild is difficult because of the elusive nature of the species (Kleiman and Brady 1978; Bekoff 2001a). However, observations of coyotes in national parks have provided insight into many aspects of the behavioral ecology of the species (Camenzind 1978; Bekoff and Wells 1980, 1981, 1986; Wells and Bekoff 1981; Gese et al. 1996a, 1996b, 1996c; Gese and Ruff 1997, 1998; Allen et al. 1999). Data on behavioral development are presented in Bekoff (1972, 1974, 1977b, 1978) and Bekoff and Dugatkin (2000). Coyotes show early development of aggressive behavior compared to wolves and most domestic dogs; they will engage in serious fights when they are only 19–24 days old (Knight 1978; Bekoff et al. 1981; Bekoff and Dugatkin 2000). The early development of rank relationships within litters appears to last up to 4.5 months (Knight 1978), but the dominance hierarchy later in life may not reflect the hierarchy observed within the litter (Bekoff 1977b; Knight 1978). General behavioral patterns (postures, gestures, tail movements, facial expressions, vocalizations) are described and discussed in Kleiman (1966), Fox (1970), Bekoff (1972, 1974, 1978), Knight (1978), Lehner (1978a, 1978b), and Wells and Bekoff (1981). Gait, stance, ear and tail position, and retraction of the lips to expose the teeth are all very important in social communication and may vary independently or together, depending on individual "mood." Comparative reviews are in Kleiman and Eisenberg (1973) and Kleiman and Brady (1978).

Social Organization. Generally, coyotes are considered less social than wolves (but see Gese et al. 1996a, 1996b). In Yellowstone National Park, high prey biomass, high survival rates, and lack of persecution has allowed formation of large packs numbering up to 10 individuals in winter (Gese et al. 1996a, 1996b). The basic social unit, even in large packs, is the dominant adult heterosexual pair, often referred to as the "alpha" pair (Bowen 1978; Bekoff and Wells 1980, 1986; Gese et al. 1996a). Associate animals will remain in the pack and possibly inherit or displace a member of the breeding pair and become an alpha themselves (Gese et al. 1996a). These associates (or beta animals) participate in territorial maintenance and pup rearing (Hatler 1995), but not to the extent of the alpha pair (Gese and Ruff 1997, 1998; Gese 2001). Other coyotes exist on the landscape outside of the resident packs and are considered transient or nomadic individuals (Camenzind 1978; Bowen 1982; Gese et al. 1988a). These transients usually travel alone over a large area, do not breed, and do not maintain a territory (Bekoff and Wells 1986; Gese and Ruff 1997, 1998; Gese 2001). Coyote packs resemble wolf packs (Bowen 1978; Bekoff and Wells 1980; Gese et al. 1996a) and it appears that differences between coyotes and wolves are quantitative rather than qualitative.

Just as with all other aspects of coyote biology, there is considerable variability in observed social organization (Bowen 1978; Bekoff and Wells 1980, 1981, 1986). In many areas, solitary individuals are frequently observed (Berg and Chesness 1978) outside of the breeding season. In other areas, such as Jackson Hole, Wyoming (Camenzind 1978; Bekoff and Wells 1980, 1981), and Jasper, Alberta (Bowen 1978), groups of coyotes are commonly observed. Prey size may be important in affecting coyote sociality (Bowen 1978; Bekoff and Wells 1980). In populations where the major prey items throughout the year are small rodents, coyotes tend to be in pairs or trios (Bekoff and Wells 1986; Gese et al. 1989a). In populations where large animals are available (e.g., elk, deer) either as live individuals or as carrion, coyotes form large groups (Bekoff and Wells 1986; Gese et al. 1996a, 1996b). However, coyote groups are not necessarily formed to capture large prey (Gese et al. 1988b), though coyotes occasionally hunt as a pair or a group (Hamlin and Schweitzer 1979; Bowyer 1987; Gese and Grothe 1995). Instead, cooperative group defense appears to be the major selective force favoring increased sociality (Berger 1978; Bowen 1978; Lamprecht 1978; Bekoff and Wells 1980). However, even within a resident pack, dominance plays a large role in access to feeding on carcasses (Gese et al. 1996b) and influences the ability of associates to remain in the pack (Gese et al. 1996a). Importantly, coyotes tend to be more social during winter, when carrion is a very important food resource (Bowen 1978; Camenzind 1978; Bekoff and Wells 1980). In areas without large ungulate carrion, increased pack size also occurs in the breeding season, which then facilitates capture of large prey (Gese et al. 1988b).

Predatory Behavior. There have been a few detailed studies of the predatory behavior of wild coyotes on small mammals (Wells and Bekoff 1982; Bekoff and Wells 1986; Gese et al. 1996b, 1996c). Predatory sequences may be divided into at least six components: search, orientation, stalk, pounce, head thrust/close search into ground cover, and rush. Pouncing is used mostly for capturing small microtine rodents, whereas the rush is used most frequently on larger animals, such as ground squirrels (Bekoff and Wells 1986; Gese et al. 1996c). Age of the animal, wind, habitat, and snow conditions (depth and hardness) all influence a coyote's ability to detect and capture small mammals (Wells and Bekoff 1982; Murray and Boutin 1991; Gese et al. 1996c). Coyotes generally hunt small mammals alone, even though the pack size may be quite large (Gese et al. 1996b, 1996c). Cooperative hunting for small mammals would be inefficient because only one individual can consume the prey item (Bowen 1981; Andelt 1985; Gese et al. 1988b). It has been shown experimentally that coyotes depend on various senses to locate prey. In order of decreasing importance, they are vision, audition, and olfaction (Wells and Lehner 1978), though these "priorities" may change depending on environmental conditions (Wells 1978).

Predatory behavior and habits of wild coyotes preying on domestic livestock have received increased attention (e.g., Henne 1977; Shivik et al. 1996; Windberg et al. 1997b; Neale et al. 1998; Sacks et al. 1999). Connolly et al. (1976) found that captive coyotes killed sheep (in confinement) only in 20 of 38 tests (52.6%); defensive behavior by sheep deterred coyotes only 31.6% of the time. Mean latency to attack was very long (47 min), with considerably variability (standard deviation = 48 min) among attacks. Mean killing time, likewise, was rather long (13 min), and considerably variable. In most instances, coyotes attacked sheep by biting the throat, and the sheep died of suffocation. Various factors influence coyote depredation rates on sheep, including breed of sheep, sheep management practices, coyote behavior, environmental factors, and depredation management programs. In general, changes in animal size and behavior, differences in group cohesiveness, sociality, grazing dispersion, attentiveness, and maternal protection all affect vulnerability to coyote predation (see review by Knowlton et al. 1999). Windberg et al. (1997b) and Bromley (2000) documented that coyotes generally killed the smallest or lightest individuals in the flock.

Cooperative hunting of adult ungulates (i.e., deer, elk, antelope) by coyotes rarely has been documented (Cahalane 1947; Murie 1951; Bruns 1970; Bowyer 1987). When coyotes attack large wild ungulates, environmental factors such as snow depth and hardness of the crust are important to the success or failure of the attempt (Gese and Grothe 1995). Presence of the alpha pair also appears to be important in the

outcome of the attack. Generally, younger animals do not participate in the attack sequence. It appears that the number of coyotes in the pack is not as important as which coyotes are involved in the attack. Even in a pack of seven coyotes, only the alpha pair was involved in attacks on large ungulates (Gese and Grothe 1995). Also, the ability of ungulates to escape into water, defensive abilities of individuals and other members of the herd or the parent, and nutritional state of the individual under attack will contribute to the outcome (Ozoga and Harger 1966; Bowyer 1987; Gese and Grothe 1995).

Communication. Coyotes communicate using auditory, visual, olfactory, and tactile cues (Lehner 1978a, 1978b). Communication by howling or vocalization is very common among coyotes (Gier 1975; Lehner 1978a, 1978b). Studies of wild coyotes have identified many different types of vocalizations (McCarley 1975; Lehner 1978a, 1978b). Seasonal and diel patterns (Laundré 1981; Walsh and Inglis 1989), lunar phase (Bender et al. 1996), and social status in the pack (Gese and Ruff 1998) also influence coyote vocalization rates. Howling among coyotes plays a role in territorial maintenance and pack spacing. It signals territorial boundaries and the presence of alpha animals, who will confront intruders and defend the territory (Gese and Ruff 1998).

Studies on olfactory communication (i.e., scent marking) among coyotes also have been conducted (Barrette and Messier 1980; Bowen and Cowan 1980; Wells and Bekoff 1981; Bekoff and Wells 1986; Gese and Ruff 1997; Allen et al. 1999). Alpha coyotes perform the majority of scent-marking duties. Rates of scent marking vary seasonally, pack size does not influence scent-marking rates, and scent marks are located more than expected along the periphery of the territory and likely contribute to territory maintenance (Bowen and Cowan 1980; Bekoff and Wells 1986; Gese and Ruff 1997). Scent marking may be a mechanism for sex recognition (Bekoff 1979a) and serve as an indicator of sexual condition, maturity, or synchrony (Bekoff and Diamond 1976). Internal information to orient members of the resident pack (Wells and Bekoff 1981) and alert dispersing animals of occupied territories also may be communicated via scent marks.

MORTALITY

Mortality Rates. Different-aged coyotes have different mortality rates. Mortality rates depend on the level of control to which a population is exposed and levels of food availability (Knowlton 1972; Todd et al. 1981; Todd and Keith 1983; Todd 1985; Gese et al. 1989a; Knowlton et al. 1999). Pups (<1 year old) and yearlings (individuals 1–2 years old) tend to have the highest mortality rates (Nellis and Keith 1976; Gese et al. 1989a). For individuals >1 year old, mortality rates vary geographically (Knowlton 1972; Nellis and Keith 1976; Bowen 1978; Andrews and Boggess 1978; Gese et al. 1989a). Mathwig (1973) found greatest life expectancy for coyotes in Iowa at 1.5 years of age and lowest life expectancy at 5.5 years. Knowlton (1972), Crabtree (1988), and Gese et al. (1989a) reported relatively high survival in 4- to 8-year-old coyotes. About 70–75% of coyote populations are 1–4 years old (see Knowlton et al. [1999] for a summary of population studies). To maintain population stability, net survival of about 33–38% seems to be necessary (Knowlton 1972; Nellis and Keith 1976).

Causes of Mortality. Most studies indicate that human activity is involved in a high proportion of the deaths of adult coyotes (Davison 1980; Tzilkowski 1980; Windberg et al. 1985; Gese et al. 1989a; Windberg 1995), although predation by large carnivores (Peterson 1995; Arjo 1998; Crabtree and Sheldon 1999) and starvation during crashes of food resources also may be substantial mortality factors. Disease also can be a factor, especially among young of the year; parvovirus killed several radio-marked pups in Yellowstone (Gese et al. 1997). Even in lightly exploited populations, most mortality is attributable to human causes. Human exploitation can be substantial in some coyote populations (Knowlton 1972; Knowlton et al. 1999).

Diseases and Parasites. Serological analyses for antibodies in coyotes have shown that they have been exposed to many diseases. In Yellowstone National Park, prevalence of antibodies against canine parvovirus (CPV) was 100% for adults, yearlings, and old pups (4–12 months old), but 0% for young pups (<3 months old) (Gese et al. 1997 [n = 110]). In Texas, Utah, Idaho, and Colorado, >70% of the coyotes had antibodies against CPV (Thomas et al. 1984 [n = 1184]; Gese et al. 1991 [n = 72]). In Georgia, 65% of 17 coyotes had antibodies against CPV (Holzman et al. 1992b). High prevalence of antibodies is often associated with a highly contagious, but nonfatal infection because prevalence is measured among survivors (Thomas et al. 1984). However, of 21 coyote pups implanted with radios in 1992 in Yellowstone, 8 of 14 deaths were from CPV infection (Gese et al. 1997).

Presence of antibodies against canine distemper virus was 88%, 54%, 23%, and 0% prevalence among adults, yearlings, old pups, and young pups, respectively, in Yellowstone National Park (Gese et al. 1997). In Texas, Trainer and Knowlton (1968) found 37% of 33 coyotes had antibodies to the virus; Guo et al. (1986) reported 56% of 228. Williams et al. (1988) reported that 50% of 10 coyotes in Wyoming tested positive for this virus. In Georgia, no coyotes were found to have been exposed (Holzman et al. 1992b).

Prevalence of canine infectious hepatitis virus antibodies was 97%, 82%, 54%, and 33% for adults, yearlings, old pups, and young pups, respectively, in Yellowstone National Park (Gese et al. 1997). Coyotes in Texas and Georgia had a lower prevalence (41–51%) of virus exposure (Trainer and Knowlton 1968; Holzman et al. 1992b). The degree to which this virus affects coyote populations is unknown.

In Yellowstone National Park, the prevalence of antibodies against the plague bacterium *Yersinia pestis* was 86%, 33%, 80%, and 7% for adults, yearlings, old pups, and young pups, respectively (Gese et al. 1997). This high prevalence was similar to results in other western states (Barnes 1982 [n = 12,405]). In contrast, coyotes in California had very low antibody prevalence (<6% of 338 coyotes sampled) (Thomas and Hughes 1992). Coyotes may become infected with *Y. pestis* by being bitten by fleas or possibly by ingesting infected rodents (Thomas et al. 1989). Infected coyotes usually do not develop clinical signs, but develop antibody titers that last about 6–8 months, making coyotes an indicator species for plague (Barnes 1982). Changes in prevalence of plague in the coyote population likely reflect prevalence of plague in the small-mammal prey base.

Serological prevalence of antibodies against *Francisella tularensis* (tularemia) was found in a coyote population in Yellowstone, but at relatively low levels (<25%) (Gese et al. 1997). In Texas, Trainer and Knowlton (1968) found no serological evidence of tularemia. In contrast, 88% of the coyotes in Idaho were seropositive (Gier et al. 1978). Coyotes may contract tularemia, but are relatively unsusceptible and will likely recover (Gier and Ameel 1959). No coyotes in Yellowstone had serological evidence of exposure to brucellosis, either *Brucella abortus* or *B. canis* (Gese et al. 1997). Similarly, coyotes in Texas and Georgia had not been exposed to brucellosis (Trainer and Knowlton 1968, Holzman et al. 1992b). Coyotes do not appear to act as significant hosts for brucellosis.

Prevalence of antibodies against leptospirosis in the coyote population in Yellowstone was low (Gese et al. 1997), similar to results for coyotes in Texas (Trainer and Knowlton 1968) and Georgia (Holzman et al. 1992b). In contrast, four of nine coyotes tested in Arizona were seropositive for leptospirosis (Drewek et al. 1981). The impact of leptospirosis on coyotes is unknown, but infected animals may survive and remain carriers for a short time.

Coyotes also carry a variety of parasites. Ectoparasites commonly found among coyotes include fleas (the most common external parasite), various ticks, mites, and lice; see Gier and Ameel (1959) and Gier et al. (1978) for species identification. Internal parasites include several species of flukes (trematodes), tapeworms (cestodes), intestinal worms (nematodes, ascarids), hookworms (ancylostomids), heartworms (filaroids), esophageal worms (spiruroids), lungworms (trichinellids), kidney worms (dioctophymoides), spiny-headed worms (acanthocephalids), protozoans, and coccidia fungus (Eads 1948; Gier and Ameel 1959; Hirsch and Gier 1974; Mitchell and Beasom 1974; Thornton et al. 1974; Conder and Loveless 1978; Gier et al. 1978;

Mercer et al. 1988; Wixsom et al. 1991; Holzman et al. 1992b). Coyotes also may carry rabies and may suffer from cardiovascular diseases, aortic aneurysms (Thornton et al. 1974), mange (Pence et al. 1983; Pence and Windberg 1994), and cancer. For reviews and taxonomic analyses of external and internal parasites, see Bekoff (1977a) and (Gier et al. 1978).

AGE ESTIMATION

Coyote age can be estimated by counting dental cementum annuli (Linhart and Knowlton 1967; Nellis et al. 1978) and coarsely estimated with tooth wear (Gier 1968). Before tooth sectioning for cementum analysis, age class (juveniles and adults) can be distinguished based on the relative pulp cavity size using radiography (Knowlton and Whittemore 2001). Roberts (1978) pointed out that there is variation in age determination from different teeth and suggested using canines in age determination. Eye lens weight, baculum weight, and thermal contraction of long tendons can also be used to estimate age accurately. Ages of young coyotes can be estimated from body mass, body length, and length of the hind foot (Gier 1968; Bekoff and Jamieson 1975; Barnum et al. 1979). The regression equation for the body mass of hand-reared pups (0–30 days of age) is $y = 0.2685 + 0.197x$; for coyotes 31–154 days of age, the equation is $y = 0.5049 + 0.0469x$ (Barnum et al. 1979). From hand-raised coyotes, the regression equations for predicting the weight of known-age coyotes are $y = -13.57 + 50.59x$ (0–30 days) and $y = 11.386 + 21.11x$ (31–154 days). The correlations between weight and age for 0–30 days and 31–154 days are 0.999 and 0.995, respectively (Barnum et al. 1979).

ECONOMIC STATUS AND MANAGEMENT

Coyotes are victims of success. By taking advantage of poorly devised domestication practices that left most livestock virtually defenseless against predation, coyotes have established a reputation for efficient and effective predation. Sheep have been selectively bred to produce animals that are suited to particular husbandry practices, regions, conditions, and cultural tastes as well as to provide food and fiber (Knowlton et al. 1999). Differences in group cohesiveness, sociality, grazing dispersion, location, attentiveness, mobility, behavior, and maternal protection all affect their vulnerability to predation (Gluesing et al. 1980; Blakesley and McGrew 1984; Knowlton et al. 1999).

Importantly, not all coyotes kill sheep. Some are never exposed to sheep (Wagner 1988), whereas others do not develop sheep-killing tendencies (U.S. Fish and Wildlife Service 1978; Timm and Connolly 1980). Shivik et al. (1996), Conner et al. (1998), and Sacks et al. (1999) described radio-collared coyotes near sheep with few lambs being killed; losses were usually attributed to the breeding, territorial coyotes. In contrast, Connolly (1988) and Windberg et al. (1997b) reported a high number of coyotes that killed and consumed livestock. In the intermountain West, Till and Knowlton (1983) and Bromley (2000) demonstrated that adult coyotes with pups were more likely to kill lambs than adults without pups. In contrast, territorial coyotes in north-coastal California kill lambs as soon as they become available in December and January, outside the pup-rearing season (Conner 1995; Sacks 1996).

Economics of Coyote Predation. The amount of livestock losses that producers attribute to coyotes is a contentious issue. Wildlife protection advocates claim that few or no depredations actually occur, whereas producers indicate losses from coyotes threaten their economic livelihood (Caine et al. 1972; Gee et al. 1977; U.S. Fish and Wildlife Service 1978; Wagner 1988; Knowlton et al. 1999). In situations where there was predator control, losses of sheep to coyotes were 1.0–6.0% for lambs and 0.1–2.0% for ewes (U.S. Fish and Wildlife Service 1978). In situations where there was no predator control, losses to coyotes ranged from 12% to 29% of lambs and from 1% to 8% of ewes (Delorenzo and Howard 1976; Brawley 1977; Henne 1977; Munoz 1977; McAdoo and Klebenow 1978; O'Gara et al. 1983). In 1994, the economic value of domestic sheep lost to predators was reported as $17.7 million (U.S. Department of Agriculture 1995). Sterner and Shumake (1978) and U.S. Department of Agriculture (1995) reported that coyotes were responsible for the majority of all sheep lost to predators. However, it is important to consider that coyote predation is not the major cause of losses (U.S. Fish and Wildlife Service 1978; Bekoff 1979b). Early et al. (1974) found that 77% of the total economic loss of sheep in 1970–1971 was due to disease (43%), unspecified causes (31%), and predators (23%).

Depredation Management. Protecting livestock or wildlife species from coyotes requires consideration of legal, social, economic, biological, technical, and ethical factors (Sterner and Shumake 1978; Wade 1978; Bekoff 1998, 2001b; Knowlton et al. 1999). Successful resolution of conflicts should consider the efficacy, selectivity, and efficiency of various procedures. Several techniques are available for reducing coyote depredations on livestock (Sterner and Shumake 1978; Wade 1978; Fall 1990; U.S. Department of Agriculture 1994). Many techniques are within the operational purview of the producers, such as nonlethal techniques. Others involve lethal control in either a preventative or corrective context. Procedures that are more benign in their effects on natural systems are typically preferred. Fall (1990), Andelt (1996), and Knowlton et al. (1999) reviewed many of the techniques for reducing coyote depredations.

Nonremoval Techniques. Several techniques have been used to deter coyotes from attacking livestock (Linhart 1984a; Wagner 1988; Fall 1990; Green et al. 1994). Whereas some methods have been successful, others are complete failures. Knowlton et al. (1999) suggested several husbandry practices that may reduce depredations, including confining or concentrating flocks during periods of vulnerability, using herders, shed lambing, removing livestock carrion from pastures, synchronizing birthing, and keeping young animals in areas with little cover and/or nearest to human activity (Robel et al. 1981; Wagner 1988).

Several types of protective fencing can exclude or reduce coyote use of an area (De Calesta and Cropsey 1978; Linhart et al. 1982; Shelton 1984, 1987; Nass and Theade 1988), but few are "coyote proof." Frightening devices that emit bursts of light or sound have deterred coyote predation on sheep in fenced pastures (Linhart et al. 1982, 1984; Linhart 1984b) and on open range (Linhart et al. 1992); however, coyotes often become habituated to such devices (Knowlton et al. 1999). Use of guard animals may reduce damage by coyotes. Dogs, llamas, and donkeys or mules are used as livestock guards (Linhart et al. 1979; Coppinger et al. 1983; Green and Woodruff 1983, 1987; Black and Green 1984; Green et al. 1984; Timm and Schmidt 1989; Powell 1993; Conner 1995).

There are no repellents and learned aversions that will deter coyote predation. A variety of gustatory, olfactory, and irritating products have been tested. Food consumption may be reduced (Hoover 1996), but predation is not (Lehner 1987; Burns and Mason 1997). Investigations of conditioned taste aversion using lithium chloride showed mixed results. Some researchers reported success at reducing food consumption (e.g., Gustavson et al. 1974, 1982; Ellins and Martin 1981; Forthman-Quick et al. 1985a, 1985b), whereas others reported no reduction of predation by coyotes (Bekoff 1975; Conover et al. 1977; Burns 1980, 1983; Burns and Connolly 1980, 1985; Bourne and Dorrance 1982).

Attempts to reduce coyote reproductive rates and population levels have been investigated, with the assumption that fewer coyotes will result in fewer depredations (Knowlton et al. 1999). Coyote reproduction was reduced using diethylstilbesterol (Balser 1964; Linhart et al. 1968), but was impractical without effective bait delivery systems. Alternatively, reproductive interference using sterilization of territorial, breeding coyotes may be an effective way to reduce depredations by coyotes (Bromley 2000) by changing the predatory behavior of adults when provisioning young (Till and Knowlton 1983). With respect to chemosterilants, both regulation (federal and state) and distribution are problematic (Steilflug et al. 1978).

Coyote Removal Techniques. When nonremoval techniques do not stop depredations, removing one or more coyotes may achieve

management objectives (Knowlton et al. 1999), especially if the removed animals are the "problem individuals" (Linnell et al. 1999). Removing one or two individuals in a small area (i.e., corrective control) may stop the problem, whereas in other cases, population reduction may be warranted. Knowlton et al. (1999) suggested that selection of the appropriate method should consider the nature of the problem, presence of a historical pattern, size of the area, season of the year, timing, efficacy, selectivity, efficiency, and animal welfare considerations (Bekoff 1998, 2001b). On small areas where specific coyotes pose the most immediate risk, calling and shooting can selectively remove coyotes killing livestock (Coolahan 1990), but requires correctly identifying the areas used by the killers.

One method that may be the most selective for removing coyotes responsible for depredations is the use of the livestock protection collar (McBride 1974, 1982; Burns et al. 1988, 1996; Connolly and Burns 1990; Connolly 1993; Rollins 1995). These devices release a toxic chemical into a coyote's mouth when the coyote attacks and punctures the collar on a sheep's neck. They are registered by the Environmental Protection Agency in seven states and require approved training and accountability programs (Moore 1985; Knowlton et al. 1999). Coyotes causing depredations also can be removed with traps, snares, and M-44 devices, but the selectivity for the offending coyote(s) is lower (Brand et al. 1995). Most depredations are attributed to territorial, dominant coyotes (Till and Knowlton 1983; Sacks 1996). Within these territories, coyotes are less vulnerable to capture devices because of their familiarity of the area (Harris 1983; Windberg and Knowlton 1990; Windberg 1996), which makes removal of offending individuals difficult (Conner et al. 1998; Sacks et al. 1999). Aerial hunting in winter is efficient and effective (Wagner and Conover 1999). However, concerns regarding the safety of pilots and gunners, selectivity of animals, and economics (but see Wagner and Conover 1999) are a matter of public debate (e.g., Finkel 1999).

Coyote Population Reduction. There may be situations in which a reduction in the number of coyotes requires serious consideration, including instances where coyotes pose a risk to other wildlife species, the spread of infectious diseases needs to be curtailed, or predation on livestock needs to be prevented when more benign techniques have been ineffective (Knowlton et al. 1999). Population reduction programs are most effective when conducted after the dominance and territorial patterns are established for the coming breeding period and before whelping, to prevent other breeding pairs from becoming established and producing offspring that season (Knowlton 1972; Connolly 1978; Knowlton et al. 1999). As noted previously, before any population reduction measures are implemented, the technical, legal, social, biological, economic, and ethical considerations as well as the efficiency, effectiveness, and selectivity of the technique should be considered.

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