COYOTE

FUR GRADING & PELT IDENTIFICATION

CHEMICAL IMMOBILIZATION

28

COYOTE

DENNIS R. VOIGT, Ontario Ministry of Natural Resources, Maple, Ontario L0J 1E0
WILLIAM E. BERG, Minnesota Department of Natural Resources, Grand Rapids, MN 55744

Thousands of references are available detailing the biology and control of coyotes (*Canis latrans*) (Dolnick et al. 1976). Despite this, however, much remains unknown about the coyote's biology. Coyotes have seldom been successfully controlled despite countless attempts. Their success at surviving human depredation is legendary; as civilization has encroached, coyotes have expanded their range. Even coyotes in urban areas are becoming more commonplace. As would be expected with any species so wide-ranging and adaptable, generalizations about coyote biology are difficult to make. A dramatic upsurge in studies during the 1970s has resulted in a much better understanding of the variability and adaptability of coyotes across North America.

DESCRIPTION

Coyotes observed in the wild are sometimes confused with other canids, such as dogs (*Canis familiaris*) or small wolves (*C. lupus lycaon*, *C. rufus*). Confusion is heightened by the possible occurrence of hybrids (wolf–dog, wolf–coyote, coyote–dog). Common names for coyotes, such as brush wolf, prairie wolf, American jackal, and God's dog (Ryden 1975), add to that confusion.

Coyotes can be distinguished from red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) by their larger size and gray pelage. Coyotes are more easily confused with wolves, which are much larger (> 20 kg [45 pounds] for adults) and have less pointed ears and muzzles and proportionately larger feet. A thorough description of the coyote can be found in Bekoff (1977).

The size and weight of coyotes are commonly overestimated, perhaps because their long pelage masks a bone structure that is lighter than that of dogs. Adult coyotes weigh 9–16 kg (20–35 pounds), with males usually about 2 kg (4 pounds) heavier than females (Gier 1968, Andrews and Boggess 1978, Berg and Chesness 1978, Bowen 1978, Todd 1978). Coyotes in northern North America are slightly heavier (15–18 kg [33–40 pounds]), with some individuals weighing more than 20 kg (Richens and Hugie 1974, Hilton 1978; A. Todd, pers. commun.; D. R. Voigt, unpubl. data). Total body length varies from 120 to 150 cm (48–60 inches), with tail lengths of about 40 cm (16 inches).

The coyote skull is typically long, with a gently sloping forehead and prominent canine teeth (Fig. 1). The carnassial teeth have developed from the upper fourth premolar and the lower first molar. The upper/lower dental formula is: incisors, 3/3; canines, 1/1; premolars, 4/4; molars, 2/3; a total of 42 teeth.

Pelage color of coyotes ranges from creamy to dark rufous, but the tawny-gray agouti pattern is the most common. Geographically, coyotes vary from a gray-black pelage in the Far North (Todd 1978) to a fulvous or lighter pelage in southern or desert areas. Throat and belly areas are light gray or white. A shoulder saddle or mane of black-tipped hairs is typical among coyotes, as are black-tipped hairs over the supracaudal gland located on the dorsal surface of the proximal third of the tail (Hildebrand 1952).

A molt occurs once a year, commencing during late spring. Coyote coats become prime during late autumn (Stains 1979, Obbard 1987). This long dense fur produces pelts that are sought for fur coats, fur trim, or other apparel.

Coyote hybridization with dogs has long been recognized (Young and Jackson 1951, Kennelly and Roberts 1969, Silver and Silver 1969), but its extent and frequency is unknown (Mengel 1971). Little evidence is available to document the effect of dog genes on coyote populations (Gipson et al. 1975). Some coyote–dog hybrids can be distinguished from dogs by using the ratio of the upper tooth row length (first premolar to last molar) to the palatal width (between the upper first molars). Animals with ratios more than 3:1 are usually coyotes; those with ratios less than 2:7 are dogs (Howard 1949, Gipson et al. 1974).

Identification of coyote–dog and coyote–wolf hybrids can seldom be done on live specimens unless the pelt color or body shape is characteristic of distinctive dog breeds. Discriminant function analyses separating species based on skull measurements are usually required (Lawrence and Bossert 1967, 1969, 1975, Gipson et al. 1974, Kolenosky and Standfield 1975, Elder and Hayden 1977, Schmitz and Kolenosky 1985). Coyote–wolf hybrids are less common because of range and social behavior differences (Kolenosky 1971). The presence of hybrids causes problems in identifying endangered wolf species or subspecies (W. Berg, unpubl. data) (see DISTRIBUTION).

DISTRIBUTION

There are 19 recognized subspecies of *C. latrans* (Young and Jackson 1951, Hall and Kelson 1959). However, Nowak (1978) suggested that range expansion and subsequent interbreeding among coyote subspecies, and among *Canis* species, may have invalidated earlier classifications.

Coyotes have evolved in North America from the Pleistocene era *Canis* that resembled today's coyote (Nowak 1978). They once ranged throughout Ontario, as evidenced by coyote bones found at archaeological sites (Peterson et al. 1953, Churcher 1959), and in Maryland and Pennsylvania (Young and Jackson 1951); however, at the time of European settlement in the western United States (c. 1830), coyotes were limited to the Great Plains and western areas. Reasons for this apparent range contraction are unclear.

Coyotes occur throughout North America, east to New

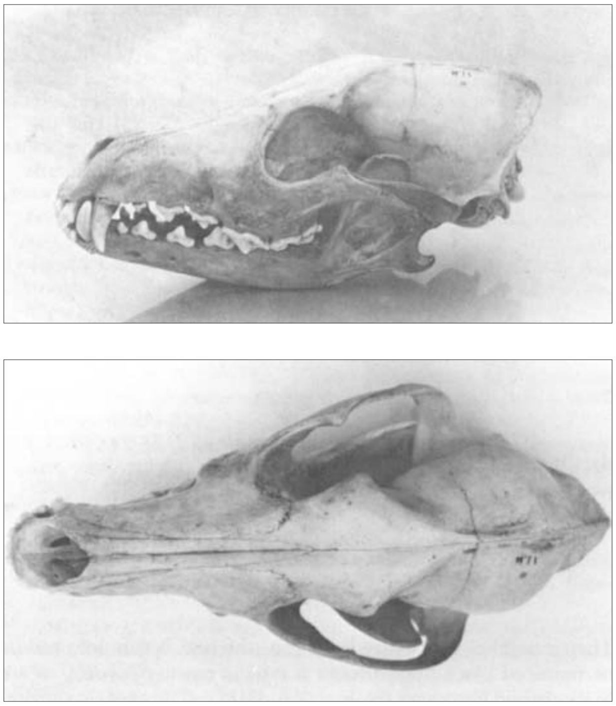


Fig. 1. A coyote skull: (top) lateral view; (bottom) dorsal view. (Photo: D. R. Voigt.)

Brunswick and Nova Scotia (Fig. 2). The populations with the highest density occur on the Plains and in the south-central United States, including Texas (see ECOLOGY – Population Density and Dynamics). They are absent in the barrens and Arctic islands of northern Canada, including much of northern Quebec and all of Newfoundland and Labrador. Coyotes are uncommon in parts of the boreal forest where wolf densities are high (northeastern Minnesota, northern Alaska, the Northwest territories, Manitoba, Ontario), but can be commonly found in the boreal forest in British Columbia, Alberta, and Saskatchewan. The distribution of coyotes in eastern North America has expanded during this century, beginning in 1900–20. Now, all eastern states and provinces have at least a small population of coyotes.

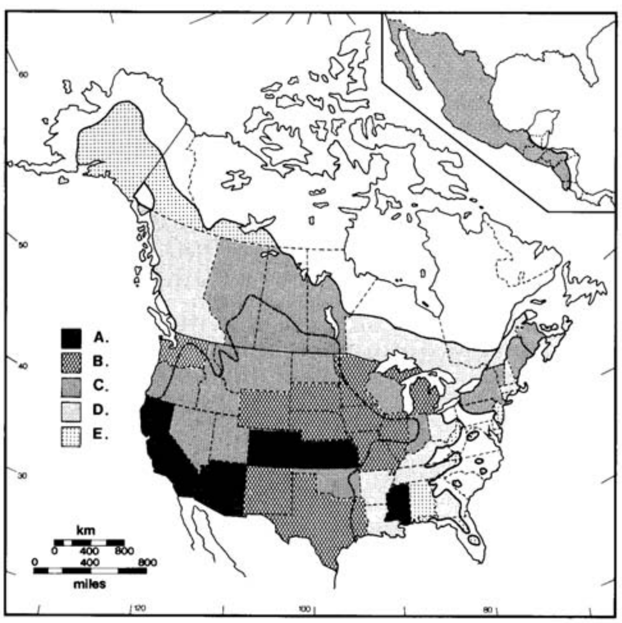


Fig. 2. Distribution and harvest density of the coyote (*Canis latrans*) in Canada and the United States for the 1983–84 trapping and hunting seasons (based on a survey by M. Novak and A. J. Satterthwaite, Ont. Minist. Nat. Resour.). Legend: (A) 2.1–10 km^2/animal harvested (area = 1,301,000 km^2); (B) 11–20 km^2/animal (2,434,000 km^2); (C) 21–100 km^2/animal (3,782,000 km^2); (D) 101–1,000 km^2/animal (2,306,000 km^2); (E) ≥ 1,001 km^2/animal (1,380,000 km^2). Total current North American range is 11,203,000 km^2. Historical (c. 1600–1800) distribution, shown by dashed line, occupied 7,300,000 km^2 (Young and Jackson1951, Mech 1970, Bekoff 1977, Kolenosky et al. 1977, McGinnis and George 1980, Henderson and Boggess 1981). (2.59 km^2 = 1 $mile^2$)

The movement of coyotes eastward has resulted in populations in the northeast (probably through hybridization with the gray wolf) that consist of a larger variety, *C. latrans* var. These populations are described for Maine (Richens and Hugie 1974, Hilton 1978), Massachusetts and New Hampshire (Lawrence and Bossert 1969), New York (Chambers et al. 1974, Severinghaus 1974), Ontario (Kolenosky et al. 1978), and Pennsylvania (McGinnis and George 1980).

In the southeastern United States, the coyotes probably hybridized with the red wolf (Paradiso and Nowak 1971, Riley and McBride 1975). Colonization of Alabama, Florida, Georgia, and Louisiana occurred at least in part as a result of human introduction (Cunningham and Dunford 1970).

Mech (1970) reviewed coyote reoccupation and expansion of its range in relation to the extirpation or absence of wolves. Coyotes were believed to be at a disadvantage when competing with the gray wolf in the eastern forests and thus were excluded. In the Plains areas, wolves and coyotes coexisted at high densities at settlement (Young and Jackson 1951). An abundance of wolf-killed bison (*Bison bison*) that coyotes could scavenge may have reduced interspecific competition. Once wolves were extirpated, coyotes occupied the entire Plains area but may not have occupied mountainous areas until after the introduction of livestock (Young and Jackson 1951).

LIFE HISTORY

Reproduction

Female coyotes have one estrus annually, which lasts 4–5 days, and breed between January and March (Kennelly 1972, 1978, Kennelly and Johns 1976). Coyotes are able to breed before their first birthday, but the percentage of yearlings conceiving litters varies from 0% to 80% in different populations (Gier 1968). In the same area, this percentage can vary from 14% to 50% over several years (Todd et al. 1981*a*). The variation in reproduction by yearlings may be influenced by food supply, winter conditions, social status, and population density (Gier 1968, Knowlton 1972, Nellis and Keith 1976, Todd 1985). Variation in the percentage of yearlings breeding causes large annual variation in the total number of coyotes breeding; the percentage of older females breeding can also vary markedly (Todd and Keith 1983, Todd 1985). In Texas the percentage of females having litters varied from 48% to 81% (Knowlton 1972).

Pups (Fig. 3) are born after a gestation period of 60–63 days. Litter size varies primarily with prey availability. Gier (1968) reported mean litter sizes of 4.8–5.1 in years with low rodent numbers, but litters of 5.8–6.2 during years with high rodent numbers. In Alberta, Todd and Keith (1976) observed correlated decreases in ovulation rates and snowshoe hare (*Lepus americanus*) abundance. Knowlton (1972) reported an increase in mean litter size from 4.3 to 6.9 with decreasing coyote densities in Texas. Mean numbers of corpora lutea for captive coyotes range from 5.6 for 2-year-olds to 7.1 for 4-year-olds (Kennelly 1978). Counts of fetuses or placental scars in western U.S. coyote control areas are as high as 14–17, suggesting compensatory reproduction (Gier 1968; J. M. Laughlin, pers. commun.). Nellis and Keith (1976) reported a 9% embryo loss between ovulation and parturition, whereas Gipson et al. (1975) reported a 27% loss. More detailed accounts of coyote reproduction can be found in Kennelly (1978) and Bekoff (1982).

Mortality

Coyotes are most vulnerable to natural and human-caused mortality during their first year, so mortality rates must be calculated separately for juvenile and adult age classes. Because most

Fig. 3. Coyote pups, age 2.5 weeks. (Photo: S. Fraser.)

mortality studies involve tagging of juveniles during late summer, the extent of mortality during the first summer is largely unknown. In Alberta, 9% of juvenile coyotes died during their first 40 days; another 68% died before they were 1 year old (Nellis and Keith 1976). In Utah, whelping-to-December losses were 41–70% (Knudsen 1976). In Kansas (Gier 1968) and Missouri (Hallett 1977), losses were approximately 50%. Windberg et al. (1985) radiocollared juvenile coyotes and estimated a mortality of 58% from 0.5 to 1.5 years.

Adult mortality rates are lower and less variable than those of juveniles. Reported annual mortality was 30% in Idaho (Hornocker et al. 1978), 35% in California (Dow 1974), 40% in Wyoming (Tzilkowski 1980), Texas (Knowlton 1972), and Iowa (Andrews and Boggess 1978), 50% in Utah (Knudsen 1976), and from 36% to 42% in Alberta (Nellis and Keith 1976). Davison (1980) found rates of 49% and 53% respectively in lightly and heavily exploited populations in Utah.

Studies using telemetry have documented causes and rates of mortality. Human-caused mortality was responsible for at least 90% of all deaths of coyotes older than 5 months in four studies (Hawthorne 1971, Clark 1972, Tzilkowski and Knowlton 1978; W. Berg, unpubl. data). In Minnesota, human-caused mortality was by trapping and snaring (48%), shooting (27%), automobiles (6%), and other causes (19%) (W. Berg, unpubl. data). In lightly exploited South Texas populations, human-caused mortality only accounted for 38% (Andelt 1985) and 57% (Windberg et al. 1985) of all deaths.

Custer and Pence (1981*a*,*b*) and Pence and Custer (1981) provided comprehensive reviews of the diseases and parasites of coyotes; Davis et al. (1970), Davis and Anderson (1971), and Gier et al. (1978) provided earlier reviews. Coyotes are affected by a variety of endoparasites. Custer and Pence (1981*a*) reviewed 53 species of helminths from different regions of North America. Cestodes were recovered most frequently but probably cause little morbidity. Heartworm (*Dirofilaria immitis*) can kill coyotes and may spread indirectly to dogs via mosquitoes. Hookworm (*Ancylostoma*) is common across the coyote's range and is debilitating to juveniles. Pence and Windberg (1984) described habitat and seasonal variables influencing helminth distributions in Texas coyote populations.

The most important viral infections in coyotes are distemper and canine hepatitis (Pence and Custer 1981). Although many other viral, bacterial, and protozoan diseases have been diagnosed in coyotes, few are significant causes of mortality. Surprisingly, rabies is not common in coyotes despite its prevalence in other coexisting furbearers such as striped skunks (*Mephitis mephitis*) and red foxes (Johnston and Beauregard 1969, Voigt and Tinline 1982).

Mites of the genus *Sarcoptes*, which cause sarcoptic mange, are the most important ectoparasites of coyotes. In a Texas epizootic, mange progressed most rapidly in juveniles but coyote population dynamics and abundance were generally unaffected (Pence et al. 1983). In an Alberta epizootic, there were no differences in sex or age between coyotes with mange and those without (Todd et al. 1981*b*). However, the body condition of mangy coyote pups was poorer than that of mangy adults. Small mammals were less important, and carrion, grain, and garbage more important, in the diets of mangy coyotes than in the diets of healthy coyotes. Todd et al. (1981*b*) suggested that mange was an important mortality factor in wild canid populations and noted that mangy coyotes sought farmyards, where they were subject to other human-caused mortality.

ECOLOGY

Habitat

A clear indication of the broad range of habitats, from grasslands to boreal forests, used by coyotes comes from the habitat descriptions in the studies cited in this chapter. Since the land-clearing era of the mid-1800s, coyotes have moved eastward along both northern and southern routes, entering previously unoccupied habitats (Nowak 1978). Encroachment in agricultural areas, such as the present movement into southwestern Minnesota (Berg and Kuehn 1986), has been continuous. Almost any habitat, including urban areas, that supports prey populations also supports coyotes (Gill 1965, Andelt 1977). Even where coyotes have been introduced by humans (e.g., Florida), they have adapted to their new habitat (Fisher 1975). Coyote distribution is limited by snow or arctic conditions (Todd et al. 1981*a*), prey size and density (with a general north to south increase in the availability of small prey) (Knowlton 1983), and competition with larger predators such as wolves (Mech 1974) and mountain lions (*Felis concolor*) (Young and Jackson 1951).

Population Density and Dynamics

The coyote is probably the most extensively studied carnivore (Bekoff 1982), and considerable research has been conducted on population dynamics. However, because of the coyote's broad geographic range, density information should not be extrapolated from one area to another. Data from scent-station indices suggest that density increases from north to south (Fig. 4). Densities also vary between prewhelping and postwhelping; postwhelping densities can be misleading (Pyrah 1984). For example, prewhelping and postwhelping densities in a Wyoming population were 0.5/km^2 (1.3/mile^2) and 1.4/km^2 (3.6/mile^2) respectively (Camenzind 1978).

Coyote densities as high as 2/km^2 (5/mile^2) have been reported in the southwestern and west-central United States. Knowlton (1972) reported a density of 0.9/km^2 (2.3/mile^2) in one area in Texas but suggested that densities of 0.2–0.4/km^2 (0.5– 1.0/mile^2) were common over large portions of the coyote's range. Andelt (1985) estimated that prewhelping coyote densities in southern Texas were 0.8–0.9 coyotes/km^2 (2.1–2.3/mile^2). He determined that fall densities were 0.9–1.0 coyote/km^2 (2.3–2.6/mile^2). Clark (1972) also reported densities from 0.1–0.3/km^2 (0.3–0.7/mile^2) in Utah and Idaho. Gier (1975) observed densities as high as 2 coyotes/km^2 (5/mile^2) in smaller areas (≤ 75 km^2 [30 miles^2]) in Kansas.

Densities are lower in the northwestern United States and western Canada. In Montana, summer densities averaged 0.4/km^2 (1.0/mile^2) (Pyrah 1984). Summer densities in one Alberta population were 0.2–0.4/km^2 (0.5–1.0/mile^2) (Bowen 1982*a*). Winter densities were 0.1/km^2 (0.3/mile^2) when snowshoe hares were scarce and 0.4–0.6/km^2 (1.0–1.5/km^2) when hares were abundant (Nellis and Keith 1976, Todd et al. 1981*a*). Coyote densities appear to be much lower in eastern and northern North America, although few studies have accurately determined densities. Winter densities in northern Minnesota were approximately 0.2/km^2 (0.5/mile^2) (Berg and Kuehn 1986) and were 0.1/km^2(0.3/mile^2) in Ontario farmland (D. R. Voigt, unpubl. data).

The dynamics of coyote populations depend on natality, mortality, emigration, and immigration (Knowlton 1983). The proportion of juveniles in autumn coyote harvests is approximately 50% (Rogers 1965, Gier 1968, Knowlton 1972, Andrews and Boggess 1978, Berg and Chesness 1978, Todd et al. 1981*a*). It is difficult to estimate precisely the proportion of juveniles in smaller research samples (Windberg et al. 1985).

Sex ratios of harvested populations usually are equal or slightly favor males (Young and Jackson 1951, Gier 1968, Boggess 1975, Berg and Chesness 1978, Davison 1980, Todd et al. 1981*a*). When populations are heavily exploited (as in the case of intensified predator control), sex ratios may favor females (Wetmore et al. 1970, Knowlton 1972). Sex ratios may favor males in declining canid populations (Kleiman and Brady 1978); Todd and Keith (1983) observed a male:female ratio of 1.4:1 during a coyote population decline.

The dynamics of a coyote population can best be understood by simulating the reproduction and mortality of a typical coyote population; more complex "models" of coyote populations have been devised by Connolly and Longhurst (1975).

Emigration and immigration also affect a population's dynamics (Knowlton 1983). Dispersal is generally from high- to low-density areas but is complex (Davison 1980, Knowlton 1983) (see discussion of dispersal in Home Ranges).

Home Ranges

Generalizations about coyote home ranges are difficult to make because methods of obtaining data and calculating home ranges differ among studies, and because home range size may differ between sexes and among seasons, habitats, and geographic areas (Smith et al. 1981, Laundré and Keller 1984). Laundré and Keller (1984) recommended that locations be determined sequentially overnight or over 24 hours, or determined sporadically at all times of the day and night. They also suggested that adequate data be collected for each of the four biological seasons described by Smith et al. (1981)—breeding, gestation, pup rearing, and dispersal. Finally, they urged investigators to examine how coyotes used their home range and how use varied with behavior, food abundance and distribution, vegetation, and other factors.

A single home range may be inhabited by a family of two or more generations, a mated pair, or a single adult, usually a female (Berg and Chesness 1978, Bekoff 1982). Home ranges are scent-marked with urine or feces year-round (Berg and Chesness 1978, Barrette and Messier 1980, Bowen and Cowan 1980, Wells and Bekoff 1981) and are therefore territories. Territorial boundary encounters may occur, although they are infrequent (Camenzind 1978, Bowen 1982*a*, Messier and Barrette 1982, Andelt 1985).

A broad range of home range sizes has been reported in the literature, from an average of 4–5 km^2 (2 $miles^2$) in Texas (Andelt 1985) to seasonal averages of 55–143 km^2 (21–55 $miles^2$) in Washington (Springer 1982). These differences are not unexpected if density varies geographically (see Population Density and Dynamics); there is a significant negative correlation between density and home range size of resident adult coyotes (Andelt 1985: Table 12). Differences among studies arise in part because some authors (e.g., Springer 1982) include all locations, whereas others (e.g., Andelt 1985) eliminate the outer 5%, which may be sallies outside the home range (Hibler 1977), when calculating home range sizes. Nevertheless, geographic variation still exists when studies using the same methods are compared (Springer 1982: Table 2). Laundré and Keller (1984) found that home range size did not differ significantly among four geographic areas representing four distinct habitats, probably because variation within studies was high and sample sizes were low.

Group size and social behavior may also influence home range size. Coyotes living in packs and defending ungulate carrion during winter may have smaller home ranges than coyotes living in pairs or alone (Bekoff and Wells 1980). In Alberta, group home range size increased as group size increased (Bowen 1982*a*); however, in Texas, group home range size did not increase as group size increased (Andelt 1985). Unusually large home ranges (> 75 km^2 [28 $miles^2$]) have been observed for solitary adults and subadults, many of which may be transient (e.g., Litvaitis and Shaw 1980, Pyrah 1984, Andelt 1985, Roy and Dorrance 1985; D. R. Voigt, unpubl. data). Transient individuals constitute 8–20% of the population (Bowen 1978, Camenzind 1978, Andelt 1985) and may be either healthy (Andelt 1985) or disabled (Camenzind 1978).

Most studies show equal male and female territory sizes, probably because most home ranges are inhabited by mated pairs (e.g., Bowen 1978, Camenzind 1978, Bekoff and Wells 1980). Laundré and Keller (1984) analyzed data from three studies and found no significant differences in home range sizes between the sexes. However, differences may occur (e.g., Litvaitis and Shaw 1980, Berg and Kuehn 1986) if solitary or nomadic individuals are included (Messier and Barrette 1982).

Prior to dispersal, the home ranges of juveniles are small and within the boundaries of their mother's home range (Litvaitis and Shaw 1980, Andelt 1985). As pups grow and become more active, their home ranges increase in size. Reported home range sizes of juveniles range from less than 5 km^2 (2 $miles^2$) in Oklahoma (Litvaitis and Shaw 1980) and Quebec (Messier and Barrette 1982) to 5–8 km^2 (2–3 $miles^2$) in Minnesota (Berg and Chesness 1978) and Ontario (D. R. Voigt, unpubl. data) to 54 km^2 (20 $miles^2$) in Washington (Springer 1982).

Dispersal movements of juvenile and subadult coyotes are generally linear, making it difficult to determine home ranges. Dispersal directions may be random (Bekoff 1982) or unidirectional (Berg and Chesness 1978). Coyotes usually begin dispersing after age 5 months and continue to disperse throughout the winter (Robinson and Cummings 1951, Knowlton 1972, Bowen 1978).

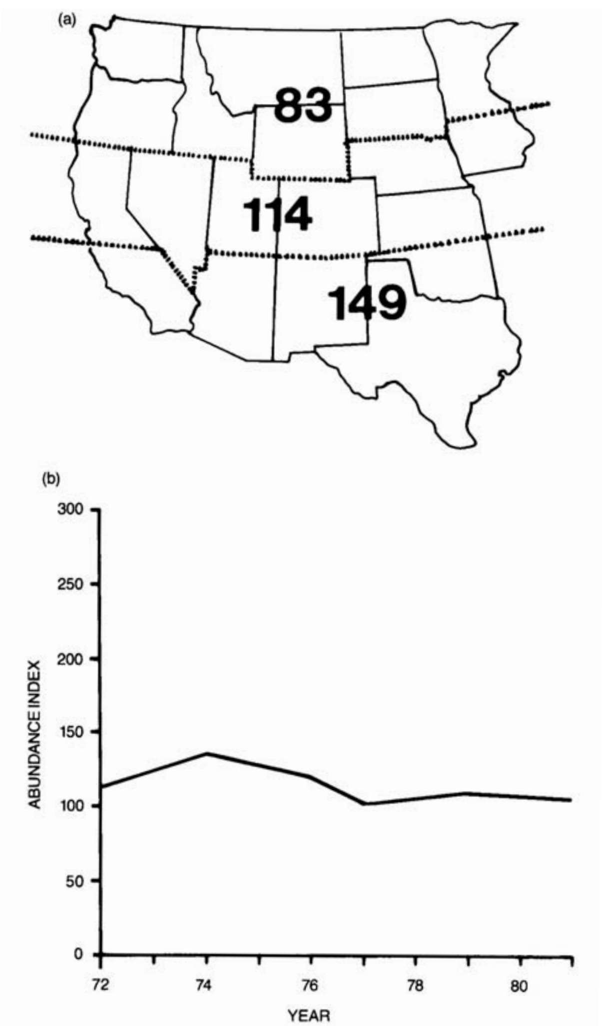


Fig. 4. (a) Mean index of coyote abundance by region from indices ot Predator Abundance in the western U.S., 1972–77 (Knowlton 1983). (b) Trends in coyote abundance from 1972–1981, all states (Source: Bean 1981).

Dispersal may be delayed in saturated populations (Bowen 1978, Camenzind 1978, Kleiman and Brady 1978, Messier and Barrette 1982, Andelt 1985), and some individuals may not disperse until their second year (Nellis and Keith 1976, Roy and Dorrance 1985). Davison (1980) found a lower proportion (31% vs. 50%) of juveniles dispersing from an exploited population than from an unexploited one.

Juveniles usually disperse alone. Dispersal distances of males were greater than those of females in Minnesota (Berg and Chesness 1978), less in California (Hawthorne 1971) and Alberta (Nellis and Keith 1976), and similar in Iowa (Andrews and Boggess 1978). Juvenile dispersal distances averaged 28–31 km (17–19 miles) in Alberta (Nellis and Keith 1976), 7 km (4 miles) in Arkansas (Gipson and Sealander 1972), 5–6 km (3–4 miles) in California (Hawthorne 1971), and 48 km (30 miles) in Minnesota (Berg and Chesness 1978). Dispersal distances may be greater from exploited than from unexploited populations (Davison 1980). Maximum dispersal distances are often greater than 100 km (60 miles) and can exceed 500 km (300 miles) (Carbyn and Paquet 1986).

FOOD HABITS

The abundance and availability of food affect both coyote density and reproduction (Gier 1968, Todd et al. 1981*a*). Fluctuations in coyote abundance have been related to abundance of rodents (Knowlton 1972), carrion (Todd and Keith 1976, Weaver 1979), snowshoe hares (Todd et al. 1981*a*, Todd and Keith 1983, Todd 1985) and black-tailed jackrabbits (*Lepus californicus*) (Clark 1972, Gross et al. 1974, Knudsen 1976, Stoddart 1977), and to social intolerances mediated by food supplies (Knowlton 1983). In general, hunting success can vary with coyote age, prey size, grass height, and environmental variables such as wind direction and snow depth (Wells and Bekoff 1982).

Rabbits (*Sylvilagus* spp.) and hares (*Lepus* spp.) are common in the winter diet of coyotes and may be the major item by both occurrence and volume (Clark 1972, Wagner and Stoddart 1972, Andrews and Boggess 1978, Hilton 1978). Small mammals, especially voles (*Microbus* spp.) and mice (*Peromyscus* spp.) are also important items in the diet of coyotes, especially during spring, summer, and fall (Andrews and Boggess 1978, Hilton 1978, Todd et al. 1981*a*). Volume or weight of voles or mice found in stomachs is often lower than that of other food items (Meriwether and Johnson 1980). Woodchucks (*Marmota monax*) were eaten by coyotes in Ontario during summer (D. R. Voigt, unpubl. data).

Livestock items are an important part of the diet of coyotes (Andrews and Boggess 1978). Predation on sheep often occurs during summer; livestock carrion is important when other prey are scarce or during winter, when carcasses remain fresh for longer periods (Todd and Keith 1976, 1983, Todd et al. 1981*a*, Todd 1985). Livestock items in coyote stomachs can seldom be identified as carrion unless the flesh is putrified or maggots and flies are present. However, observations of feeding coyotes, ground- and radio-tracking, and observations by farmers suggest that most livestock consumed, except sheep, is carrion.

In both western and eastern North America, big game constitutes a significant portion of the coyote's diet. Whereas wolves generally eat beaver-size or larger prey, the coyote's body size, bioenergetics, and flexible social behavior enable them to prey on animals of all sizes. Generally, coyote food habits and tracking studies have shown that much of the big game consumed by coyotes is carrion (Niebauer and Rongstad 1977, Berg and Chesness 1978, Huegel 1979, Weaver 1979). However, when snow impairs deer (*Odocoileus* spp.) movement, coyotes may be important predators on adult deer (Messier and Barrette 1985). Hilton (1978) also found that coyotes in Maine can effectively capture prey as large as a white-tailed deer (*O. virginianus*). In other areas, many of the deer killed during early winter are fawns, and most adult killed are either old or affected with abnormalities (Ozoga and Harger 1966, Hamilton 1974). Fawns are frequently consumed as both carrion and prey during early summer (Cook et al. 1971, Salwasser 1974, Berg and Chesness 1978, Bowen 1978, Kie et al. 1979, Litvaitis and Shaw 1980). In Minnesota the predation rate is estimated at one fawn per coyote annually (Berg and Kuehn 1986). The overall impact of coyotes on deer populations is unknown; however, fawn survival increased after coyote control programs were implemented in Texas (Beasom 1974) and Oklahoma (Stout 1982).

Food habits studies show an extensive list of other food items, but they invariably include plant items such as fruits, berries, and seeds (Andrews and Boggess 1978, Berg and Chesness 1978, Todd et al. 1981*a*). Coyotes will cache surplus food and mark caching sites with urine (Harrington 1982).

In summary, coyotes consume a variety of foods year-round but emphasize small mammals, fawns, plants, and assorted birds and invertebrates during summer. Winter diet emphasizes larger items such as deer (either prey or carrion), livestock carrion, or locally abundant lagomorph species.

BEHAVIOR

Mated pairs of coyotes or groups of adult coyotes plus pups form the basic family unit (Camenzind 1978, Bowen 1978, 1981, Althoff 1978, Andelt and Gipson 1979, Andelt et al. 1979, Bekoff and Wells 1980, 1981, 1982, Althoff and Gipson 1981, Messier and Barrette 1982, Andelt 1985). Mated pairs of coyotes may produce pups each year, and both adults often assist in the care of young (Ryden 1975). In larger groups, nonbreeding adults also help to care for pups (Camenzind 1978, Andelt et al. 1979, Bekoff and Wells 1980, Andelt 1985). Helpers that do not breed have been documented for many other canids (Macdonald 1979, Moehlman 1979).

The number of coyotes in groups traveling and foraging together is largest during winter, but family social units are largest during summer when pups, their parents, and nonbreeding adults are together at dens and rendezvous sites (Camenzind 1978, Bowen 1981, Messier and Barrette 1982, Andelt 1985). During winter, groups of one, two, or three or more coyotes were respectively observed on 43%, 34%, and 23% of observations in Quebec (Messier and Barrette 1982) and 62%, 30%, and 8% of observations in Minnesota (Berg and Chesness 1978). Pairs of coyotes constituted 87% of observations in Wisconsin (Huegel 1979). Pairs became more prevalent during late winter in other studies (Hilton 1978, Messier and Barrette 1982).

In some instances, group behavior can be related to pup-rearing duties, predation on large prey that may require group hunting strategies, or defense of carrion (Camenzind 1978, Bowen 1981). High densities (saturated populations) also favor maintenance of groups through delayed dispersal (Messier and Barrette 1982, Andelt 1985). Bekoff and Wells (1980) and Bowen (1981) found a positive correlation between group size and prey size. Their studies in Wyoming and Alberta showed that coyotes in larger groups preyed on big game, although they still fed extensively on carrion. However, Andelt (1985) did not observe a positive correlation between group size and prey size. In all these studies, larger groups of three to eight coyotes were related adults, yearlings, and young.

Coyotes are active day and night, with peaks in activity occurring at sunrise or sunset. Generally, activity and movements such as foraging are greatest at night (Ozoga and Harger 1966, Smith et al. 1981; D. R. Voigt, unpubl. data). Andelt (1985) found that daytime activity increased during the breeding season. Gipson and Sealander (1972) found that pups were more active than adults during the day.

The availability of food and such spatial behavior as territoriality appear to be important mechanisms regulating coyote population size (Knowlton 1983). Radio-tracking studies suggest that territoriality occurs in almost all populations of coyotes, although not all individual coyotes are territorial. Adult females, mated pairs, and groups of coyotes defend territories. Food availability appears to influence territory size, but the prey of coyotes may also determine group size (see also Home Ranges). Wolves can influence the movements and distribution of coyotes by preying on them or causing avoidance behavior (Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982, Berg and Kuehn 1986);

coyotes can affect red foxes (Voigt and Earle 1983) and kit foxes (*Vulpes macrotis*) in a similar manner.

Coyote communication by auditory, olfactory, and physical means was summarized by Lehner (1978*a*,*b*). The most common auditory communication between packs or individuals is a variety of yips, barks, and howls (Gier 1975). Olfactory communication is done through scent-marking by fecal and urine deposits and anal sac secretions (Young and Jackson 1951). Coyotes also visually communicate through a variety of displays and activities to show antagonism, dominance, and greetings (Fox 1975, Lehner 1978*a*,*b*).

MANAGEMENT

Sexing and Aging Techniques

Live coyotes or pelts are most easily sexed using external characteristics (presence or absence of a penis hole or nipples). Pelt size cannot be used to separate sexes. Carcasses can be sexed using internal or external genitalia or less reliably by using skull morphology (Gier 1968). The sagittal crest is considerably more developed in males than in females.

Young less than 30 days old can be aged to day from weights (Barnum et al. 1979, Bekoff and Jamieson 1975). Juveniles as old as 8 months can be aged to month by body weight or length of feet, head, or body (Gier 1968). These determinations are derived from regressions given by Bekoff (1982:448–449).

Most live or dead specimens are aged using dental characteristics. Radiographs of teeth are used to separate juveniles (< 1 year old) from adults (> 1 year old) (Grue and Jensen 1976, Kuehn and Berg 198l). Juveniles have an open root canal, adults a closed or partially closed root canal (Fig. 5). Fur harvesters can distinguish juveniles by cutting a canine with a hacksaw and checking for the open root canal. Adults are most accurately aged by preparing tooth sections to count cementum annuli (Linhart and Knowlton 1967, Allen and Kohn 1976, Nellis et al. 1978, Bowen 1982*b*). The age of animals released for study can be estimated approximately up to age 8 years by tooth wear patterns (Gier 1968) or, more reliably, by removing a premolar to count cementum annuli (Roberts 1978; D. R. Voigt, unpubl. data). Canines are usually extracted from carcasses to count cementum annuli, as they provide more accurate age estimates than do premolars (Roberts 1978).

Censusing and Estimating Population Numbers

Wolfe (1973) summarized the methodology and biases of most population survey techniques for coyotes. Basically, these techniques are (1) direct counts or catch–mark–release; (2) counts of dens, tracks, or droppings; (3) direct counts from aircraft; (4) catch-per-unit-effort surveys, questionnaires, and bounty payments; and (5) elicited scent-station and vocalization responses (Knowlton and Stoddart 1984). None provide an accurate total count of coyotes over a wide area, and most provide only indices of population change. Some of these techniques are described below in order of their reliability and usefulness.

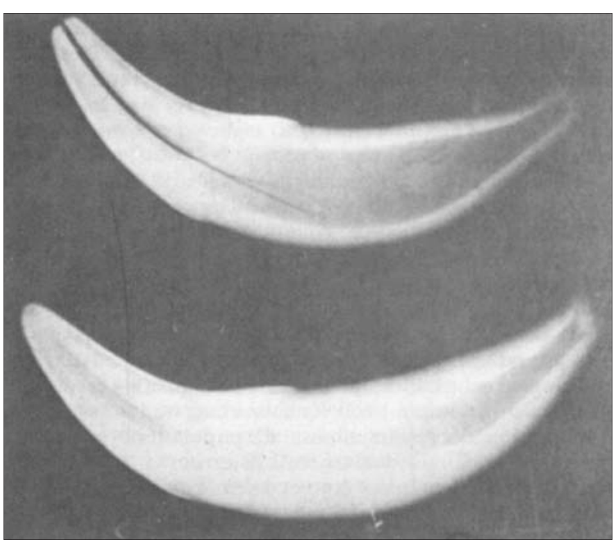


Fig. 5. Radiographs of canine teeth from a 9-month-old coyote (top) showing open root canal and from an adult (bottom) showing partially closed canal. (Photo: W. Berg.)

The most commonly used and most statistically refined (Roughton 1979) technique in the United States is the scent-station index, described by Linhart and Knowlton (1975) and revised by Roughton and Sweeny (1982). Scent stations rely on a response to an olfactory stimulus to estimate relative coyote abundance over large areas. The highly standardized method uses stations of sifted soil 90 cm (3 feet) in diameter, spaced at 0.5-km (0.3 miles) intervals, with a small plaster-of-paris disk impregnated with a standardized scent (available from the U.S. Dep. Agric. Supply Depot, Pocatello, Idaho). The basic sampling unit is a 4.3-km (2.7 miles) line containing 10 stations; these stations are checked for tracks after 1 night. An index is calculated as the number of stations containing coyote tracks, divided by the total operative station nights, then multiplied by 1,000. Sampling is affected by environmental variables such as frozen ground, heavy rainfall, or snowfall. Scent-stations were originally devised for coyotes but are also useful for other carnivores (Sumner and Hill 1980, Conner et al. 1983).

A recently developed radiotracer technique that shows great promise is radioisotope-marking of individual animals and subsequent analysis of feces (Pelton and Marcum 1977, Davison 1980, Kruuk et al. 1980, Crabtree et al. 1985). Individuals can be injected intramuscularly or intraperitoneally with gamma-emitting radioactive isotopes. The proportion of marked to unmarked feces can be used to construct a population estimate, and certain radioactive labels on feces can identify individual coyotes. Reliable estimates can be obtained with adequate sample sizes, but workforce and equipment costs are high.

Another index uses vocalization responses to electronic siren wails, recordings, or people imitating the howls of coyotes or wolves at listening stations along a survey route (Wenger and Cringan 1978, Okoniewski and Chambers 1984, Pyrah 1984, Dekker 1985). The number of stations with responses is divided by the total number of stations, then multiplied by 100, to provide an index value (Goff 1979). Unfortunately, many factors affect responses of coyotes (Wenger and Cringan 1977, 1978), such as environmental variables, coyote density, or individual responsiveness (Lehner 1978*a*,*b*). Seasonal changes in the probability of coyotes responding to howls or sirens are known to occur but have not been quantified; however, vocalizations may provide reliable indices of coyote abundance in small areas (Wenger and Cringan 1978). Based on his experiments in Iowa, Andrews (1979) suggested that vocalizations had some advantages over scent stations, especially in the eastern United States, where domestic dogs are common and roads are heavily traveled.

Most agencies use harvest data and catch-per-effort data derived from questionnaires and report cards to estimate coyote population trends (Clark and Andrews 1982). These data are subject to biases arising from response rates, pelt prices, and the honesty of the respondents. Predator control and bounty data may provide an index of population trends if capture effort is consistent over time.

Another survey method that has been used in more northern areas is a winter track index (Todd and Keith 1976, Goff 1979), which consists of counts of the number of coyote tracks crossing a trail or road over a standard survey distance. This method has many of the same problems as the elicited response indices and has not been calibrated with actual population counts. Time since last snowfall, depth of snow, and other environmental variables may influence results.

Clark (1972) used a combination of labor-intensive methods to estimate coyote density and population trends in a large study area in Utah and Idaho. One method was a modification of the Petersen estimate (Bailey 1951). During each May of the 5-year study, coyote pups were taken from dens, eartagged, and released.

A second sample was taken in the same area by trapping during August and September, and the number of tagged pups captured was used to estimate the density of coyote pups. A minimum count estimate was also obtained by summing the number of pups tagged during spring and the number of untagged pups trapped during autumn. Finally, the juvenile coyote population was estimated from the number of coyote litters raised on the study area (derived from den searches) multiplied by mean litter size (from adult female carcasses). Juvenile coyote totals were added to adult totals for a total population estimate. Todd et al. (1981*a*) also used observations of marked coyotes (Lincoln index = Petersen estimate) to provide population estimates in Alberta.

Estimating Population Growth

An understanding of coyote population dynamics requires incorporation of various techniques for determining (1) fecundity, which includes in utero reproductive data such as counts of corpora lutea, placental scars, and fetuses, pregnancy rate, and litter size; (2) postparturition mortality data such as natural and human-caused mortality for juveniles and adults; and (3) emigration and immigration data (Storm and Tzilkowski 1982, Knowlton 1983).

Fecundity.–Preparturition fecundity data can only be obtained from examination of carcasses. Spring collections provide data on the current breeding season but are often unobtainable. Collections must be made from a particular coyote population or study area; samples from a wide geographic range are not useful. Corpora lutea counts can be made visually from fresh material (Gier 1968, Todd et al. 1981*a*); preserved material may require staining and sectioning (Humason 1972). Examination of placental scars, which appear as darkened segments on uterine horns, provides information on the mean litter size and the proportion of each age class of females that whelped during the previous spring. Because some uteri may have multiple scars in various stages of resorption (Gier 1968), only the largest and darkest scars (representing the most recent pregnancy) should be counted. Viable and resorbed fetuses may be difficult to separate (Kennelly 1978). Age-specific pregnancy rates and litter sizes may be related to food abundance (Gier 1968, Todd and Keith 1983) or behavior (see LIFE HISTORY and FOOD HABITS). Time is often wasted trying to determine age-specific in utero productivity for each age class; because 2-year-old and older females usually contribute most to annual reproduction (Gier 1968, Knowlton 1972), division into juvenile, yearling, and adult (≥ 2 years) classes usually suffices.

Mortality.–Postparturition harvest data can be obtained from harvest surveys, registration data, and research. Again, all have inherent sampling and design biases; however, harvest data are the most reliably obtained component of all mortality data.

Nonharvest mortality is more difficult to determine and can be substantial. Approximately 50–60% of juvenile coyotes may die between birth and autumn (see LIFE HISTORY). Until radiotelemetry, the extent of nonharvest mortality was largely unknown or biased by factors affecting recapture and tag recovery. Telemetry has made it possible to calculate mortality rate from the total number of transmitter days (Trent and Rongstad 1974, Heisey and Fuller 1985). Windberg et al. (1985) calculated similar mortality rates from both telemetry and eartag population estimates.

Population Growth Rate.–Stable populations occur when natality and mortality are balanced; a stable population and a stable age structure are often assumed in life table analyses (Caughley 1977). Harvest and actual population sex- and age structures often differ because of differences in harvest vulnerability between the sexes or among age classes (Gier 1968, Windberg et al. 1985). Coyote juveniles, for example, may be harvested at rates 10–20% greater than their occurrence in the population. Therefore, harvest age- and sex ratios must be adjusted to represent actual population ratios.

In areas with relatively stable prey populations, coyote populations are also likely to be relatively stable (Andelt 1985). Carcasses need only be collected for 2–3 years to obtain sufficient age, sex, and reproductive data for analysis. Where prey populations fluctuate greatly, reproductive and mortality parameters may vary greatly and continued coyote carcass collections through at least one prey population cycle are necessary (Gier 1968, Todd and Keith 1983).

Population data can be analyzed using computer simulation models (Connolly and Longhurst 1975, Connolly 1978, Johnson 1982). Coyote population models begin with a specific number of coyotes and chronologically incorporate known and estimated reproductive and mortality parameters for each desired sex- and age class (Fig. 6). A broad range of future harvest levels can be simulated to evaluate harvest strategies.

Regulating the Harvest

Unlike harvests of most other furbearers, coyote harvests are rarely manipulated through quotas, or even through closure of season or area. Since the time of European settlement, the coyote has been considered a predator that must be controlled (Young and Jackson 1951); harvests are seldom regulated to ensure an optimum sustained yield. Intensive control efforts or increased harvests resulting from higher pelt prices may increase recruitment rates through compensatory reproduction. Several studies (e.g., Robinson 1956 cited in Connolly 1978, Knowlton 1972, Connolly 1978) have documented 30–100% increases in reproductive rates or densities in areas where coyotes are intensively controlled. Models must account for this phenomenon; using such adjustments, Connolly and Longhurst (1975) calculated that harvesting 75% of a coyote population annually would not exterminate the population in 50 years. Thus, harvest and control of coyotes may result in populations with high recruitment rates without regulations designed for that purpose. Mortality and reproductive rates from several studies suggest that recruitment of coyotes is high in many populations (Knowlton 1972, 1983,

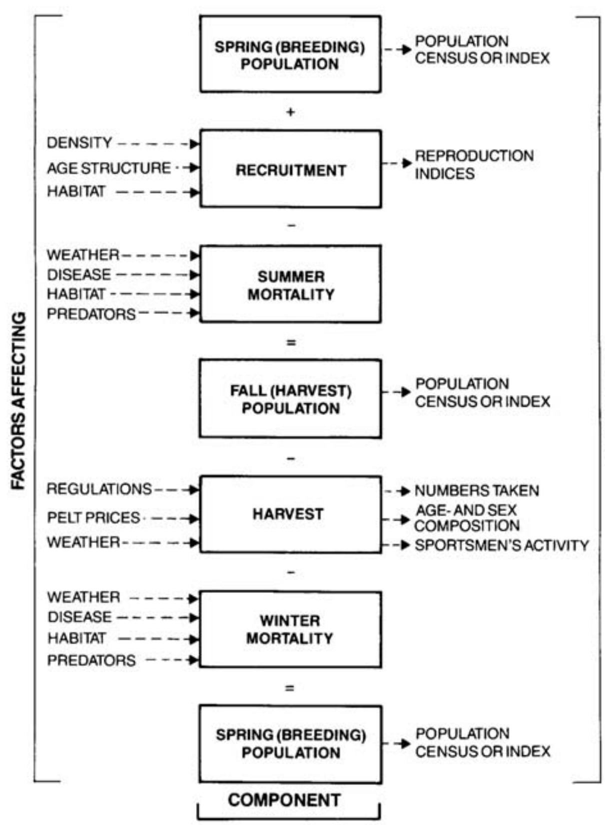


Fig. 6. Input data required to simulate factors affecting a coyote population during 1 year; for other years the model recycles, using that year's inputs (Source: Johnson 1982).

Mathwig 1973, Nellis and Keith 1976, Berg and Chesness 1978, Bowen 1978).

Most coyotes are harvested from mid-November to mid-February, when pelts are prime (Stains 1979, Obbard 1987), regardless of whether the harvest is regulated. Enforcement problems occur when coyotes are unprotected, or when coyote seasons span the more limited seasons of other furbearers. Problems also occur where trade of wolves is prohibited and wolf pelts are sold as coyote pelts. Harvest and trapper effort statistics are valuable as simple indicators of population trends, but comparisons among years should be adjusted for pelt price and standardized dollar value. Erickson (1982) discussed the use of commonly used trader transaction data to estimate total harvest but cautioned against evaluating population dynamics without other information. Erickson (1981) also determined the variables influencing coyote harvests in Missouri; these included relative population levels and market demand for pelts. Harvests could not be related to climatic variables.

Live Capture Methods

Most coyotes are captured live in steel foothold traps or neck or body snares despite the potential of other methods (for a review see Nellis 1968). Foothold traps are controversial and a common target for criticism because they are often nonselective (Beasom 1974, Turkowski et al. 1984) and may injure coyotes (Linhart et al. 1981, Olson et al. 1986). Several adaptations to the traps (sizes 2, 3, and 4) have made them more acceptable. Tranquilizer tabs have been attached to trap jaws; Balser (1965) used 750 mg of diazepam per trap and reported that 62% of captures were relatively injury-free. Because diazepam is often unavailable, Linhart et al. (1981) experimented with four other trap tabs (one, the McBride tab, is commercially available) and found that they reduced injuries significantly. Inexpensive and commercially available pan tension devices using springs, shear pins, and pads significantly reduce capture of smaller nontarget animals (Linhart et al. 1981, Turkowski et al. 1984). Padded jaw traps reduce damage to coyote feet and enable nontarget animals to be released (Olson et al. 1986), although they are less efficient in frozen or heavy soils (Linhart et al. 1981).

Snares are cheaper than steel traps, and where legal, they can be used where environmental conditions preclude trapping (Wade 1978). Snares can be adapted for live capture by adding swivels and a lock that prevents the noose from closing to a diameter less than 27 cm (10.5 inches) (Nellis 1968). The foot snare combines the speed of a trap and the humaneness of a snare (Berchielli and Tullar 1980, Novak 1981). This device enables nontarget species to be released and causes very few injuries to coyotes (Novak 1981). Traps, snares, and other holding devices should be checked once and preferably twice daily (Berchielli 1981).

Aerial darting (Baer et al. 1978) and net-gunning (Barrett et al. 1982) are promising live capture methods in open areas. These methods may be inexpensive, costs for capturing mule deer (*Odocoileus hemionus*) using a similar technique were $12–$18 per deer (Gerlach et al. 1986). Control methods using ultralight aircraft (Knight et al. 1986) do not appear promising for live capture. Aerial delivery systems and capture from snowmobiles can only be used in open areas and have little potential for forested areas.

For most handling procedures such as eartagging, measuring, and radiocollaring, chemical immobilization is recommended. Coyotes have been tranquilized with intramuscular injections of phencyclidine hydrochloride (Sernalyn) at 2 mg/kg and promazine hydrochloride (Sparine) at 4 mg/kg (Berg and Chesness 1978). Ketamine hydrochloride (Ketaset, Vetaset, Vetalar) has been used alone or with a variety of drugs, such as acepromazine maleate (Atravet) (Baer et al. 1978, Hallett et al. 1979). Ratios of seven parts ketamine to three parts Atravet are effective at dosages of 20 mg/kg (Voigt and Lotimer 1981).

Economic Importance

Coyotes are esthetically (Henderson and Boggess 1981), economically, and ecologically beneficial; they are also detrimental. The coyote is a valuable furbearer: approximately 500,000 pelts are harvested annually in North America (Deems and Pursley 1978) (Fig. 7). Although pelt prices vary with area and demand, a mean pelt price as low as $20 generates $10 million in coyote pelt sales, or approximately 2% of the total North American raw fur value (Deems and Pursley 1983).

The coyote's ecological value for controlling small mammals (Clark 1972, Wagner and Stoddart 1972, Keith et al. 1977), particularly rodents, and its detrimental ecological effect on game species, are treated elsewhere in this volume (Andelt 1987). Andelt (1987) also detailed domestic livestock losses and depredation control; a summary follows.

Amory (1973) estimated that coyote control cost the U.S. government $8 million in 1971. Individual states have spent more than $1 million annually. The ongoing research directed at coyote control methods may be unprecedented for any other wildlife species, despite inconclusive cost–benefit analyses.

The coyote is an important predator of domestic sheep, causing $19 million in losses in 1978 (U.S. Fish Wildl. Serv. 1978). During the last 20–25 years, sheep production has almost halved in North America as a result of a variety of factors such as synthetic fiber replacement, production costs, and losses to predators. Although coyotes have been implicated in 46–100% of sheep predator losses, Sterner and Shumake (1978) and Bekoff (1979) found little evidence that coyote predation is the primary factor responsible for decreased sheep production.

Balser (1974) reviewed research on damage assessment and suggested that trends in the sheep industry should be monitored, losses documented in areas with and without coyote control, and areas with high losses described and analyzed in detail. Many studies on coyote ecology and predatory behavior have been funded because of sheep losses (Connolly et al. 1976). Recent investigations have focused on fencing (deCalesta 1983) and aversive conditioning using tainted meat (Olsen and Lehner 1978) or toxic eartags or collars on sheep (Lehner et al. 1976).

The delivery of chemosterilants in baits has been attempted, but reproductive inhibitors either were not effective, had short duration (Balser 1964, Linhart et al. 1968, Gates et al. 1976), or were not species-specific. At present, chemosterilants have no field application.

Chemicals as lethal agents have historically been widely used, but they are now seldom used in the United States because of the 1969 Environmental Policy Act, the Endangered Species Act, and the 1972 Presidential ban on poison, or in Canada as a result of similar legislation. Consequently, research has been directed only at techniques that were relatively species-specific and safe, such as cyanide-loaded ejectors (e.g., the M–44) (Matheny 1976). Poisoning relies on depopulation, which has been shown both in

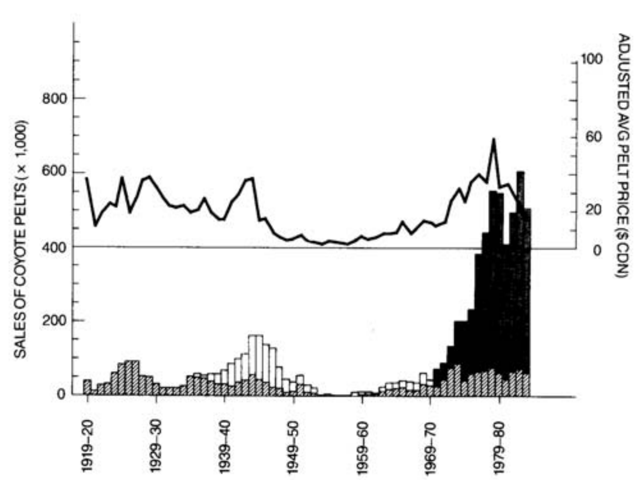


Fig. 7. Sales of coyote pelts in Canada (hatched bars) and the United States (pre-1970, open bars; post-1970, stippled bars). Solid line shows adjusted average price (1970 $CDN = 1.0). Source: Obbard et al. (1987).

practice and in computer simulation studies (Connolly and Longhurst 1975) to have insufficient long-lasting effects. Since the 1972 Presidential ban on poison, no general increase in coyotes has been documented in the United States (Bean 198l) (Fig. 4).

Trapping, snaring, and hunting coyotes can be effective where livestock losses are not heavy and widespread. These methods can be directed at specific problem individuals; their effectiveness depends on the skill of the controllers and the magnitude of the problem.

Livestock husbandry practices have the potential to reduce coyote predation. Shepherds are expensive but may assist in reducing losses (Davenport et al. 1973). Confinement of sheep is intuitively appealing when economical; however, Dorrance and Roy (1976) documented cases where greater losses of confined sheep occurred because the sheep were unable to escape their predators, and Andelt et al. (1980:377) suggested that "surplus killing may be related to the abundance of domestic prey that have lost many avoidance strategies." The use of Komondor and Great Pyrenees guard dogs has been successful in some areas (Green et al. 1984).

Sterner and Shumake (1978:322) summarized the current coyote–livestock problem: "Although there is an urgent need for the development of an effective, safe, selective, cost-efficient, socially-acceptable, and easily-used technique, our review indicates that no quick solution to the coyote damage-control problem is imminent."

CONCLUSIONS

The coyote is North America's most intensively studied and wide-ranging canid. It has survived and expanded its range despite control attempts that have surpassed those for any species in North America. Many challenges remain to make control and harvest methods more humane, efficient, selective, and economical. Some control efforts may have increased the fecundity and mobility of coyotes. Major research questions, aside from those involved with improving control techniques, address effectiveness of control measures and the response of coyote populations. These findings would benefit agencies concerned with regulating the coyote fur harvest.

Because coyotes have an almost continent-wide distribution, care must be exercised when making generalizations. The extent of natural mortality and the effect of coyotes on their prey is poorly understood except in a few situations, yet these factors are essential to understanding regulation of coyote populations. Almost in spite of additional research, the coyote promises to retain many mysteries and perhaps adapt further. A minimal goal of students of the coyote is to understand the effects of management activities on coyote populations.

LITERATURE CITED

ALLEN, S. H., AND S. C. KOHN. 1976. Assignment of age-classes in coyotes from canine cementum annuli. J. Wildl. Manage. 40:796–797.

ALTHOFF, D. P. 1978. Social and spatial relationships of coyote families and neighboring coyotes. M.S. Thesis, Univ. Nebraska, Lincoln. 80pp.

———, AND P. S. GIPSON. 1981. Coyote family spatial relationships with reference to poultry losses. J. Wildl. Manage. 45:641–649.

AMORY, C. 1973. Little brother of the wolf. Am. Way 6:18–20.

ANDELT, W. F. 1977. Ecology of the urban coyote. Proc. Nebraska Acad. Sci. 87:5.

———. 1985. Behavioral ecology of coyotes in south Texas. Wildl. Monogr. 94. 45pp.

———. 1987. Coyote predation. *In* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

———, D. P. ALTHOFF, R. M. CASE, AND P. S. GIPSON. 1980. Surplus-killing by coyotes. J. Mammal. 61:377–378.

———, ———, AND P. S. GIPSON. 1979. Movements of breeding coyotes with emphasis on den site relationships. J. Mammal. 60:568–575.

———, AND P. S. GIPSON. 1979. Home range, activity, and daily movements of coyotes. J. Wildl. Manage. 43:944–951.

ANDREWS, R. D. 1979. Furbearer population surveys and techniques: their problems and uses in Iowa. Pages 45–55 *in* Proc. Midwest Furbearer Conf. Kansas State Univ., Coop. Ext. Serv., Manhattan.

———, AND E. K. BOGGESS. 1978. Ecology of coyotes in Iowa. Pages 249–265 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

BAER, C. H., R. E. SEVERSON, AND S. B. LINHART. 1978. Live capture of coyotes from a helicopter with ketamine hydrochloride. J. Wildl. Manage. 42:452–454.

BAILEY, N. T. J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38:293–306.

BALSER, D. S. 1964. Management of predator populations with anti-fertility agents. J. Wildl. Manage. 28:352–358.

———. 1965. Tranquilizer tabs for capturing wild carnivores. J. Wildl. Manage. 29:438–442.

———. 1974. A review of coyote control research. Proc. Vertebr. Pest Conf. 6:171–177.

BARNUM, D. A., J. S. GREEN, J. T. FLINDERS, AND N. L. GATES. 1979. Nutritional levels and growth rates of hand-reared coyote pups. J. Mammal. 60:820–823.

BARRETT, M. W., J. L. NOLAN, AND L. D. ROY. 1982. Evaluation of a hand-held net-gun to capture large mammals. Wildl. Soc. Bull. 10:108–114.

BARRETTE, C., AND F. MESSIER. 1980. Scent-marking in free-ranging coyotes, *Canis latrans*. Anim. Behav. 28:814–819.

BEAN, J. R. 1981. Indices of predator abundance in the western United States, 1981. U.S. Fish Wildl. Serv., Wildl. Res. Cent., Denver, Colo. 103pp.

BEASOM, S. L. 1974. Relationships between predator removal and white-tailed deer net productivity. J. Wildl. Manage. 38:854–859.

BEKOFF, M. 1977. *Canis latrans*. Mamm. Species No. 79. 9pp.

———. 1979. Coyote damage assessment in the west: review of a report. BioScience 29:754.

———. 1982. Coyote. Pages 447–459 *in* J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America: biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, Md.

———, AND R. JAMIESON. 1975. Physical development in coyotes (*Canis latrans*), with a comparison to other canids. J. Mammal. 56:685–692.

———, AND M. C. WELLS. 1980. The social ecology of coyotes. Sci. Am. 242(4):130–148.

———, AND ———. 1981. Behavioral budgeting by wild coyotes: the influence of food resources and social organization. Anim. Behav. 29:794–801.

———, AND ———. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defense. Z. Tierpsychol. 60:281–305.

BERCHIELLI, L. T., JR. 1981. A comparison of three trap visiting schedules. Pages 1686–1690 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND B. F. TULLAR, JR. 1980. Comparison of a leg snare with a standard leg-gripping trap. New York Fish and Game J. 27:63–71.

BERG, W. E., AND R. A. CHESNESS. 1978. Ecology of coyotes in northern Minnesota. Pages 229–247 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

———, AND D. W. KUEHN. 1986. Elusive coyote. Minn. Volunteer 49(287):9–13.

BOGGESS, E. K. 1975. Some population parameters of Iowa coyotes and an analysis of reported livestock losses. M.S. Thesis, Iowa State Univ., Ames. 94pp.

BOWEN, W. D. 1978. Social organization of the coyote in relation to prey size. Ph.D. Thesis, Univ. British Columbia, Vancouver. 230pp.

———. 1981. Variation in coyote social organization: the influence of prey size. Can. J. Zool. 59:639–652.

———. 1982*a*. Home range and spatial organization of coyotes in Jasper National Park, Alberta. J. Wildl. Manage. 46:201–216.

———. 1982*b*. Determining age of coyotes, *Canis latrans*, by tooth sections and tooth-wear patterns. Can. Field-Nat. 96:339–341.

———, AND I. MCT. COWAN. 1980. Scent marking in coyotes. Can. J. Zool. 58:473–480.

CAMENZIND, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267–294 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

CARBYN, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Can. Field-Nat. 96:176–183.

———, AND P. C. PAQUET. 1986. Long distance movement of a coyote from Riding Mountain National Park. J. Wildl. Manage. 50:89.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London, U.K. 234pp.

CHAMBERS, R. E., P. N. GASKIN, R. A. POST, AND S. A. CAMERON. 1974. The coyote. Conservationist 29(2):5–7.

CHURCHER, C. S. 1959. The specific status of the New World red fox. J. Mammal. 40:513–520.

CLARK, F. W. 1972. Influence of jackrabbit density on coyote population change. J. Wildl. Manage. 36:343–356.

CLARK, W. R., AND R. D. ANDREWS. 1982. Review of population indices applied in furbearer management. Pages 11–22 *in* G. C. Sanderson, ed. Midwest furbearer management. Proc. Symp. 43rd Midwest Fish and Wildl. Conf., Wichita, Kans.

CONNER, M. C., R. F. LABISKY, AND D. R. PROGULSKE, JR. 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes, and opossums. Wildl. Soc. Bull. 11:146–152.

CONNOLLY, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327–345 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

———, AND W. M. LONGHURST. 1975. The effects of control on coyote populations: a simulation model. Univ. California, Div. Agric. Sci., Bull. 1872. 37pp.

———, R. M. TIMM, W. E. HOWARD, AND W. M. LONGHURST. 1976. Sheep killing behavior of captive coyotes. J. Wildl. Manage. 40:400–407.

COOK, R. S., M. WHITE, D. O. TRAINER, AND W. C. GLAZENER. 1971. Mortality of young white-tailed deer fawns in South Texas. J. Wildl. Manage. 35:47–56.

CRABTREE, R. L., F. G. BURTON, T. R. GARLAND, AND W. H. RICKARD. 1985. Carnivore studies: a new individual marking system. Abstract No. 0132/133 *in* W. B. Fuller, M. T. Nietfeld, and N. A. Harris, eds. Abstracts of papers and posters presented at Fourth International Theriological Conference, Edmonton, Alta.

CUNNINGHAM, V. D., AND R. D. DUNFORD. 1970. Recent coyote record from Florida. Q. J. Fla. Acad. Sci. 33:279–280.

CUSTER, J. W., AND D. B. PENCE. 1981*a*. Host–parasite relationships in the wild Canidae of North America. I. Ecology of helminth infections in the genus *Canis*. Pages 730–759 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND ———. 1981*b*. Ecological analyses of helminth populations of wild canids from the Gulf Coastal prairies of Texas and Louisiana. J. Parasitol. 67:289–307.

DAVENPORT, J. W., J. E. BOWNS, J. P. WORKMAN, AND D. B. NIELSEN. 1973. Assessment of sheep losses. Pages 3–17 *in* F. H. Wagner, ed. Final report to Four Corners Regional Commission Predator Control Study. Utah State Univ., Contract FCRC No. 621-366-044.

DAVIS, J. W., AND R. C. ANDERSON, editors. 1971. Parasitic diseases of wild mammals. Iowa State Univ. Press, Ames. 364pp.

———, L. H. KARSTAD, AND D. O. TRAINER, editors. 1970. Infectious diseases of wild mammals. Iowa State Univ. Press, Ames. 421pp.

DAVISON, R. P. 1980. The effect of exploitation on some parameters of coyote populations. Ph.D. Thesis, Utah State Univ., Logan. 153pp.

DECALESTA, D. S. 1983. Building an electric antipredator fence. Oregon State Univ., Pacific Northwest Coop. Ext. Publ. 225. 11pp.

DEEMS, E. F., JR., AND D. PURSLEY, editors. 1978. North American furbearers: their management, research and harvest status in 1976. Univ. Maryland Press, College Park. 171pp.

———, AND ———. 1983. North American furbearers: a contemporary reference. Int. Assoc. Fish and Wildl. Agencies, Maryland Dep. Nat. Resour. 223pp.

DEKKER, D. 1985. Responses of wolves, *Canis lupus*, to simulated howling on a homesite during fall and winter in Jasper National Park, Alberta. Can. Field-Nat. 99:90–93.

DOLNICK, E. H., R. L. MEDFORD, AND R. J. SCHIED. 1976. Bibliography on the control and management of the coyote and related canids with selected references on animal physiology, behavior, control methods, and reproduction. Protein Nutrition Lab., Agric. Res. Serv., Beltsville, Md. 247pp.

DORRANCE, M. J., AND L. D. ROY. 1976. Predation losses of domestic sheep in Alberta. J. Range Manage. 29:457–460.

DOW, R. J. 1974. Analysis of four populations of free-ranging coyotes in California. M.S. Thesis, Univ. California, Davis. 54pp.

ELDER, W. H., AND C. M. HAYDEN. 1977. Use of discriminant function in taxonomic determination of canids from Missouri. J. Mammal. 58:17–24.

ERICKSON, D. W. 1981. Furbearer harvest mechanics: an examination of variables influencing fur harvest in Missouri. Pages 1469–1491 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———. 1982. Establishing and using furbearer harvest information. Pages 53–65 *in* G. C. Sanderson, ed. Midwest furbearer management. Proc. Symp. 43rd Midwest Fish and Wildl. Conf., Wichita, Kans.

FISHER, J. 1975. The Plains dog moves east. Natl. Wildl. 13(2):1417.

FOX, M. W., editor. 1975. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co., New York, N.Y. 508pp.

FULLER, T. K., AND L. B. KEITH. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. J. Mammal. 62:403–405.

GATES, N. L., C. S. CARD, V. EROSCHENKO, AND C. V. HULET. 1976. Insensitivity of the coyote testis to orally administered cadmium. Theriogenology 5:281–288.

GERLACH, T. P., M. R. VAUGHAN, AND W. R. MYTTON. 1986. Comparison of two helicopter types for net-gunning mule deer. Wildl. Soc. Bull. 14:70–72.

GIER, H. T. 1968. Coyotes in Kansas. Rev. ed. Kansas State Coll., Agric. Exp. Stn. Bull. 393. 118pp.

———. 1975. Ecology and behavior of the coyote (*Canis latrans*). Pages 247–262 *in* M. W. Fox, ed. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co., New York, N.Y.

———, S. M. KRUCKENBERG, AND R. J. MARLER. 1978. Parasites and diseases of coyotes. Pages 37–71 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

GILL, D. A. 1965. Coyote and urban man: a geographic analysis of the relationship between the coyote and man in Los Angeles. M.A. Thesis, Univ. California, Los Angeles. 114pp.

GIPSON, P. S., I. K. GIPSON, AND J. A. SEALANDER. 1975. Reproductive biology of wild *Canis* (Canidae) in Arkansas. J. Mammal. 56:605–612.

———, AND J. A. SEALANDER. 1972. Home range and activity of the coyote (*Canis latrans frustror*) in Arkansas. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 26:82–95.

———, ———, AND J. E. DUNN. 1974. The taxonomic status of wild *Canis* in Arkansas. Syst. Zool. 23:1–11.

GOFF, G. 1979. Analysis and evaluation of three indices of eastern coyote abundance. M.S. Thesis, State Univ. New York, Syracuse. 101pp.

GREEN, J. S., R. A. WOODRUFF, AND T. T. TUELLER. 1984. Livestock-guarding dogs for predator control: costs, benefits, and practicality. Wildl. Soc. Bull. 12:44–50.

GROSS, J. E., L. C. STODDART, AND F. H. WAGNER. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildl. Monogr. 40. 68pp.

GRUE, H., AND B. JENSEN. 1976. Annual cementum structures in canine teeth in arctic foxes (*Alopex lagopus* (L.)) from Greenland and Denmark. Dan. Rev. Game Biol. 10(3):1–12.

HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. 2 vols. The Ronald Press Co., New York, N.Y. 1,081pp.

HALLETT, D. L. 1977. Post-natal mortality, movements, and den sites of Missouri coyotes. M.S. Thesis, Univ. Missouri, Columbia. 144pp.

———, J. D. RHOADES, AND R. R. PADDLEFORD. 1979. Immobilization of coyotes with ketamine and propiomazine. J. Am. Vet. Med. Assoc. 175:1007–1008.

HAMILTON, W. J., JR. 1974. Food habits of the coyote in the Adirondacks. New York Fish and Game J. 21:177–181.

HARRINGTON, F. H. 1982. Urine marking at food and caches in captive coyotes. Can. J. Zool. 60:776–782.

HAWTHORNE, V. M. 1971. Coyote movements in Sagehen Creek Basin, northeastern California. Calif. Fish and Game 57:154–161.

HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668–674.

HENDERSON, F. R., AND E. K. BOGGESS. 1981. Coyotes as an aesthetic and renewable resource. Utah State Univ., Logan. 52pp.

HIBLER, S. J. 1977. Coyote movement patterns with emphasis on home range characteristics. M.S. Thesis, Utah State Univ., Logan. 114pp.

HILDEBRAND, M. 1952. The integument in Canidae. J. Mammal. 33:419–428.

HILTON, H. 1978. Systematics and ecology of the eastern coyote. Pages 209–228 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

HORNOCKER, M. G., S. CHERRY, J. P. MESSICK, J. S. WHITMAN, AND J. COPELAND. 1978. Dynamics of predation upon a raptor prey base in the Snake River Birds of Prey Natural Area, Idaho. U.S. Bureau Land Manage., Contract No. 52500-CT5-1004. 95pp.

HOWARD, W. E. 1949. A means to distinguish skulls of coyotes and domestic dogs. J. Mammal. 30:169–171.

HUEGEL, C. N. 1979. Winter ecology of coyotes in northern Wisconsin. M.S. Thesis, Univ. Wisconsin, Madison. 32pp.

HUMASON, G. L. 1972. Animal tissue techniques. 3rd ed. W. H. Freeman and Co., San Francisco, Calif. 641pp.

JOHNSON, D. H. 1982. Population modeling for furbearer management. Pages 25–37 *in* G. C. Sanderson, ed. Midwest Furbearer management. Proc. Symp. 43rd Midwest Fish and Wildl. Conf., Wichita, Kans.

JOHNSTON, D. H., AND M. BEAUREGARD. 1969. Rabies epidemiology in Ontario. Bull. Wildl. Dis. Assoc. 5:357–370.

KEITH, L. B., A. W. TODD, C. J. BRAND, R. S. ADAMCIK, AND D. H. RUSCH. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Int. Congr. Game Biol. 13:151–175.

KENNELLY, J. J. 1972. Coyote reproduction. I. The duration of the spermatogenic cycle and epididymal sperm transport. J. Reprod. Fertil. 31:163–170.

———. 1978. Coyote reproduction. Pages 73–93 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

———, AND B. E. JOHNS. 1976. The estrous cycle of coyotes. J. Wildl. Manage. 40:272–277.

———, AND J. D. ROBERTS. 1969. Fertility of coyote–dog hybrids. J. Mammal. 50:830–831.

KIE, J. G., M. WHITE, AND F. F. KNOWLTON. 1979. Effects of coyote predation on population dynamics of white-tailed deer. Pages 65–82 *in* D. L. Drawe, ed. Proc. 1st Welder Wildl. Found. Symp., Corpus Christi, Tex.

KLEIMAN, D. G. AND C. A. BRADY. 1978. Coyote behavior in the context of recent canid research: problems and perspectives. Pages 163–188 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

KNIGHT, J. E., C. L. FOSTER, V. W. HOWARD, AND J. G. SCHICKEDANZ. 1986. A pilot test of ultralight aircraft for control of coyotes. Wildl. Soc. Bull. 14:174–177.

KNOWLTON, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. J. Wildl. Manage. 36:369–382.

———. 1983. Coyote population dynamics: another look. Pages 93–111 *in* F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds. Symposium on the natural regulation of wildlife populations. Univ. Idaho For., Wildl. and Range Exp. Stn., Moscow.

———, AND L. C. STODDART. 1984. Feasibility of assessing coyote abundance on small areas. U.S. Fish Wildl. Serv., Washington, D.C. 14pp.

KNUDSEN, J. J. 1976. Demographic analysis of a Utah–Idaho coyote population. M.S. Thesis, Utah State Univ., Logan. 195pp.

KOLENOSKY, G. B. 1971. Hybridization between wolf and coyote. J. Mammal. 52:446–449.

———, AND R. O. STANDFIELD. 1975. Morphological and ecological variation among gray wolves (*Canis lupus*) of Ontario, Canada. Pages 62–72 *in* M. W. Fox, ed. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co., New York, N.Y.

———, D. R. VOIGT, AND R. O. STANDFIELD. 1978. Wolves and coyotes in Ontario. Rev. ed. Ont. Minist. Nat. Resour., Wildl. Branch, Maple. 35pp.

KRUUK, H., M. GORMAN, AND T. PARRISH. 1980. The use of ^{65}Zn for estimating populations of carnivores. Oikos 34:206–208.

KUEHN, D. W., AND W. E. BERG. 1981. Use of radiographs to identify age-classes of fisher. J. Wildl. Manage. 45:1009–1010.

LAUNDRÉ, J. W., AND B. L. KELLER. 1984. Home range size of coyotes: a critical review. J. Wildl. Manage. 48:127–139.

LAWRENCE, B., AND W. H. BOSSERT. 1967. Multiple character analysis of *Canis lupus*, *latrans*, and *familiaris*, with a discussion of the relationships of *Canis niger*. Am. Zool. 7:223–232.

———, AND ———. 1969. The cranial evidence for hybridization in New England *Canis*. Breviora 330:1–13.

———, AND ———. 1975. Relationships of North American *Canis* shown by a multiple character analysis of selected populations. Pages 73–86 *in* M. W. Fox, ed. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co., New York, N.Y.

LEHNER, P. N. 1978*a*. Coyote communication. Pages 127–162 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

———. 1978*b*. Coyote vocalizations: a lexicon and comparison with other canids. Anim. Behav. 26:712–722.

———, R. KRUMM, AND A. T. CRINGAN. 1976. Tests for olfactory repellents for coyotes and dogs. J. Wildl. Manage. 40:145–150.

LINHART, S. B., H. H. BRUSMAN, AND D. S. BALSER. 1968. Field evaluation of an antifertility agent, Stilbestrol, for inhibiting coyote reproduction. Trans. North Am. Wildl. and Nat. Resour. Conf. 33:316–327.

———, G. J. DASCH, AND F. J. TURKOWSKI. 1981. The steel leg-hold trap: techniques for reducing foot injury and increasing selectivity. Pages 1560–1578 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND F. F. KNOWLTON. 1967. Determining age of coyotes by tooth cementum layers. J. Wildl. Manage. 31:362–365.

———, AND ———. 1975. Determining the relative abundance of coyotes by scent station lines. Wildl. Soc. Bull. 3:119–124.

LITVAITIS, J. A., AND J. H. SHAW. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. J. Wildl. Manage. 44:62–68.

MACDONALD, D. W. 1979. "Helpers" in fox society. Nature 282:69–71.

MATHENY, R. W. 1976. Review and results of sodium cyanide spring loaded ejector mechanism (SCSLEM) experimental programs. Proc. Vertebr. Pest Conf. 7:161–177.

MATHWIG, H. J. 1973. Food and population characteristics of Iowa coyotes. Iowa State J. Res. 47:l67–189.

MCGINNIS, H., AND J. L. GEORGE. 1980. The eastern coyote—Pennsylvania's not-so-new animal. Pa. Game News 51(6):17–22.

MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Nat. Hist. Press, Garden City, N.Y. 384pp.

———. 1974. *Canis lupus*. Mamm. Species No. 37. 6pp.

MENGEL, R. M. 1971. A study of dog–coyote hybrids and implications concerning hybridization in *Canis*. J. Mammal. 52:316–336.

MERIWETHER, D., AND M. K. JOHNSON. 1980. Mammalian prey digestibility by coyotes. J. Mammal. 61:774–775.

MESSIER, F., AND C. BARRETTE. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Can. J. Zool. 60:1743–1753.

———, AND ———. 1985. The efficiency of yarding behaviour by white-tailed deer as an antipredator strategy. Can. J. Zool. 63:785–789.

MOEHLMAN, P. D. 1979. Jackal helpers and pup survival. Nature 277:382–383.

NELLIS, C. H. 1968. Some methods for capturing coyotes alive. J. Wildl. Manage. 32:402–405.

———, AND L. B. KEITH. 1976. Population dynamics of coyotes in central Alberta, 1964–68. J. Wildl. Manage. 40:389–399.

———, S. P. WETMORE, AND L. B. KEITH. 1978. Age-related characteristics of coyote canines. J. Wildl. Manage. 42:680–683.

NIEBAUER, T. J., AND O. J. RONGSTAD. 1977. Coyote food habits in northwestern Wisconsin. Pages 237–251 *in* R. L. Phillips and C. Jonkel, eds. Proc. 1975 Predator Symp., Mont. For. and Conserv. Exp. Stn., Univ. Montana, Missoula.

NOVAK, M. 1981. The foot-snare and the leg-hold trap: a comparison. Pages 1671–1685 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

NOWAK, R. M. 1978. Evolution and taxonomy of coyotes and related *Canis*. Pages 3–16 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

OBBARD, M. E. 1987. Fur grading and pelt identification. *In* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

———, J. G. JONES, R. NEWMAN, A. BOOTH, A. J. SATTERTHWAITE, AND G. LINSCOMBE. 1987. Furbearer harvests in North America. *In* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

OKONIEWSKI, J. C., AND R. E. CHAMBERS. 1984. Coyote vocal response to an electronic siren and human howling. J. Wildl. Manage. 48:217–222.

OLSEN, A., AND P. N. LEHNER. 1978. Conditioned avoidance of prey in coyotes. J. Wildl. Manage. 42:676–679.

OLSON, G. H., S. B. LINHART, R. A. HOLMES, G. J. DASCH, AND C. B. MALE. 1986. Injuries to coyotes caught in padded and unpadded steel foothold traps. Wildl. Soc. Bull. 14:219–223.

OZOGA, J. J., AND E. M. HARGER. 1966. Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Manage. 30:809–818.

PARADISO, J. L., AND R. M. NOWAK. 1971. A report on the taxonomic status and distribution of the red wolf. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl. 145. 36pp.

PELTON, M. R., AND L. C. MARCUM. 1977. The potential use of radioisotopes for determining densities of black bears and other carnivores. Pages 221–236 *in* R. L. Phillips and C. Jonkel, eds. Proc. 1975 Predator Symp., Mont. For. and Conserv. Exp. Stn., Univ. Montana, Missoula.

PENCE, D. B., AND J. W. CUSTER. 1981. Host–parasite relationships in the wild Canidae of North America. II. Pathology of infectious diseases in the genus *Canis*. Pages 760–845 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND L. A. WINDBERG. 1984. Population dynamics across selected habitat variables of the helminth community in coyotes, *Canis latrans*, from south Texas. J. Parasitol. 70:735–746.

———, ———, B. C. PENCE, AND R. SPROWLS. 1983. The epizootiology and pathology of sarcoptic mange in coyotes, *Canis latrans*, from south Texas. J. Parasitol. 69:1100–1115.

PETERSON, R. L., R. O. STANDFIELD, E. H. MCEWEN, AND A. C. BROOKS. 1953. Early records of the red and the gray fox in Ontario. J. Mammal. 34:126–127.

PYRAH, D. 1984. Social distribution and population estimates of coyotes in north-central Montana. J. Wildl. Manage. 48:679–690.

RICHENS, V. B., AND R. D. HUGIE. 1974. Distribution, taxonomic status, and characteristics of coyotes in Maine. J. Wildl. Manage. 38:447–454.

RILEY, G. A., AND R. T. MCBRIDE. 1975. A survey of the red wolf (*Canis rufus*). Pages 263–277 *in* M. W. Fox, ed. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co., New York, N.Y.

ROBERTS, J. D. 1978. Variation in coyote age determination from annuli in different teeth. J. Wildl. Manage. 42:454–456.

ROBINSON, W. B., AND M. W. CUMMINGS. 1951. Movement of coyotes from and to Yellowstone National Park. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl. 11. 17pp.

ROGERS, J. G. 1965. Analysis of the coyote population of Dona Ana County, New Mexico. M.S. Thesis, New Mexico State Univ., Las Cruces. 39pp.

ROUGHTON, R. D. 1979. Developments in scent station methodology. Pages 17–44 *in* Proc. Midwest Furbearer Conf. Kansas State Univ., Coop. Ext. Serv., Manhattan.

———, AND M. W. SWEENY. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. J. Wildl. Manage. 46:217–229.

ROY, L. D., AND M. J. DORRANCE. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. J. Wildl. Manage. 49:307–313.

RYDEN, H. 1975. God's dog—a celebration of the North American coyote. Viking Press, New York, N.Y. 315pp.

SALWASSER, H. 1974. Coyote scats as an indicator of time of fawn mortality in the North Kings deer herd. California Fish and Game 60:84–87.

SCHMITZ, O. J., AND G. B. KOLENOSKY. 1985. Wolves and coyotes in Ontario: morphological relationships and origins. Can. J. Zool. 63:1130–1137.

SEVERINGHAUS, C. W. 1974. Notes on the history of wild canids in New York. N.Y. Fish and Game J. 21:117–125.

SILVER, H., AND W. T. SILVER. 1969. Growth and behavior of the coyote-like canid of northern New England with observations on canid hybrids. Wildl. Monogr. 17. 41pp.

SMITH, G. J., J. R. CARY, AND O. J. RONGSTAD. 1981. Sampling strategies for radio-tracking coyotes. Wildl. Soc. Bull. 9:88–93.

SPRINGER, J. T. 1982. Movement patterns of coyotes in south central Washington. J. Wildl. Manage. 46:191–200.

STAINS, H. J. 1979. Primeness in North American furbearers. Wildl. Soc. Bull. 7:120–124.

STERNER, R. T., AND S. A. SHUMAKE. 1978. Coyote damage-control research: a review and analysis. Pages 297–325 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

STODDART, L. C. 1977. Population dynamics, movements and home range of black-tailed jackrabbits (*Lepus californicus*) in Curlew Valley, northern Utah. U.S. Energy Res. Dev. Adm., Contract No. E(11-1)-1329, Annu. Prog. Rep. 42pp.

STORM, G. L., AND W. M. TZILKOWSKI. 1982. Furbearer population dynamics: a local and regional management perspective. Pages 69–90 *in* G. C. Sanderson, ed. Midwest furbearer management. Proc. Symp. 43rd Midwest Fish and Wildl. Conf., Wichita, Kans.

STOUT, G. G. 1982. Effects of coyote reduction on white-tailed deer productivity on Fort Sill, Oklahoma. Wildl. Soc. Bull. 10:329–332.

SUMNER, P. W., AND E. P. HILL. 1980. Scent stations as indices of abundance in some furbearers of Alabama. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 34:572–583.

TODD, A. W. 1978. The coyote. Bull. Can. Assoc. Humane Trapping 1978(Summer):3–5.

———. 1985. Demographic and dietary comparisons of forest and farmland coyote, *Canis latrans*, populations in Alberta. Can. Field-Nat. 99:163–171.

———, J. R. GUNSON, AND W. M. SAMUEL. 1981*b*. Sarcoptic mange: an important disease of coyotes and wolves of Alberta, Canada. Pages 706–729 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND L. B. KEITH. 1976. Responses of coyotes to winter reductions in agricultural carrion. Alberta Dep. Rec., Parks and Wildl., Fish and Wildl. Div., Wildl. Tech. Bull. 5. 32pp.

———, AND ———. 1983. Coyote demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 47:394–404.

———, ———, AND C. A. FISCHER. 1981*a*. Population ecology of coyotes during a fluctuation of snowshoe hares. J. Wildl. Manage. 45:629–640.

TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459–472.

TURKOWSKI, F. J., A. R. ARMISTEAD, AND S. B. LINHART. 1984. Selectivity and effectiveness of pan tension devices for coyote foothold traps. J. Wildl. Manage. 48:700–708.

TZILKOWSKI, W. M. 1980. Mortality patterns of radio-marked coyotes in Jackson Hole, Wyoming. Ph.D. Thesis, Univ. Massachusetts, Amherst. 67pp.

———, AND F. F. KNOWLTON. 1978. Man-caused mortality of coyotes marked in Grand Teton National Park. Pages 164–168 *in* R. Iltner, D. R. Potter, J. K. Agee, and S. Anchell, eds. Proc. Recreational Impact on Wildlands Conf., Univ. Washington, Seattle.

U.S. FISH AND WILDLIFE SERVICE. 1978. Predator damage in the west: a study of coyote management alternatives. U.S. Fish Wildl. Serv., Washington, D.C. 168pp.

VOIGT, D. R., AND B. D. EARLE. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 47:852–857.

———, AND J. S. LOTIMER. 1981. Radio tracking terrestrial furbearers: system design, procedures, and data collection. Pages 1151–1188 *in* J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.

———, AND R. L. TINLINE. 1982. Fox rabies and trapping: a study of disease and fur harvest interaction. Pages 139–156 *in* G. C. Sanderson, ed. Midwest furbearer management. Proc. Symp. 43rd Midwest Fish and Wildl. Conf., Wichita, Kans.

WADE, D. A. 1978. Coyote damage: a survey of its nature and scope, control measures and their application. Pages 347–368 *in* M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

WAGNER, F. H., AND L. C. STODDART. 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. J. Wildl. Manage. 36:329–342.

WEAVER, J. L. 1979. Influence of elk carrion upon coyote populations in Jackson Hole, Wyoming. Pages 152–157 *in* M. S. Boyce and L. D. Hayden-Wing, eds. Symposium on North American elk: ecology, behavior and management, Univ. Wyoming, Laramie.

WELLS, M. C., AND M. BEKOFF. 1981. An observational study of scent-marking in coyotes, *Canis latrans*. Anim. Behav. 29:332–350.

———, AND ———. 1982. Predation by wild coyotes: behavioral and ecological analyses. J. Mammal. 63:118–127.

WENGER, C. R., AND A. T. CRINGAN. 1977. Biotelemetry in studying responses of coyotes to electronic sirens. Int. Conf. Wildl. Biotelemetry 1:126–l30.

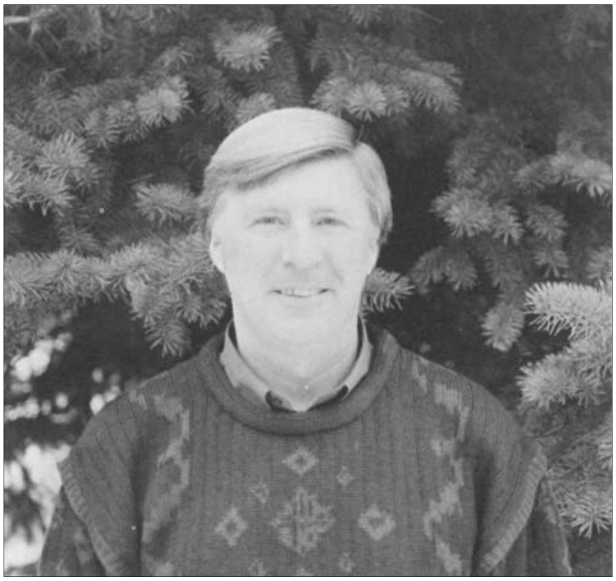
———, AND ———. 1978. Siren-elicited coyote vocalizations: an evaluation of a census technique. Wildl. Soc. Bull. 6:73–76.

WETMORE, S. P., C. H. NELLIS, AND L. B. KEITH. 1970. A study of winter coyote hunting in Alberta with emphasis on use of snowmobiles. Alta. Dep. Lands Forests, Fish and Wildl. Div., Wildl. Tech. Bull. 2. 22pp.

WINDBERG, L. A., H. L. ANDERSON, AND R. M. ENGEMAN. 1985. Survival of coyotes in southern Texas. J. Wildl. Manage. 49:301–307.

WOLFE, G. J. 1973. A literature review of coyote census techniques. Colorado State Univ., Fort Collins. 24pp.

YOUNG, S. P., AND H. H. T. JACKSON. 1951. The clever coyote. The Stackpole Co., Harrisburg, Pa., and The Wildl. Manage. Inst., Washington, D.C. 411pp.



(Photo: P. Bachmann.)

DENNIS R. VOIGT is a research scientist at the Ontario Ministry of Natural Resources Wildlife Research Station in Maple, Ont. He is currently supervising a field study of population ecology and effects of winter feeding on white-tailed deer, and working with a modeling team to develop a spatial simulation model of fox rabies ecology and control.Voigt received an M.Sc. from the University of Guelph, writing his thesis on gray wolves, and has done research on bears, beavers, and humane trap development. Since 1974 he has supervised ecological studies of red foxes, coyotes, raccoons, and skunks as part of a research project to develop an oral vaccine for rabies control in foxes.

– at time of first publication (1987)

(Photo: K. Kerr.)

WILLIAM E. BERG received his B.S. in wildlife management and M.S. in wildlife ecology from the University of Minnesota. His master's research focused on the ecology of moose in northwestern Minnesota. A wildlife biologist with the Minnesota Department of Natural Resources (MDNR), Berg was at the Red Lake Wildlife Management Area in Roosevelt, Minn., from 1971 to 1974, then joined the MDNR Forest Wildlife Populations and Research Group in Grand Rapids, Minn. At both Roosevelt and Grand Rapids he studied moose and sharp-tailed grouse populations, and since 1974 his research has also emphasized the predators of grouse and moose, such as coyotes, wolves, bobcats, and fishers.

– at time of first publication (1987)