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Canis latrans. By Marc Bekoff

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Canis latrans Say, 1823

Coyote

Canis latrans Say, *in* James, 1823:168. Type locality Engineer Cantonment, about 19.2 km SE present town of Blair, Washington Co., Nebraska.
Canis ochropus Eschscholtz (1829:1). Type locality Sacramento River Valley near Sacramento, California.
Lyciscus cagottis Hamilton Smith (1839:164). Type locality Río Frio, west slope of Mount Iztaccihuatl, México.
Canis frustror Woodhouse (1850–51:147). Type locality Red fork of the Arkansas River, probably near 97° west longitude, near Perkins, Payne Co. (now Cimarron River), Oklahoma.
Canis lestes Merriam (1897:25). Type locality Toyabe Mountains near Cloverdale, Nye Co., Nevada.
Canis mearnsi Merriam (1897:29). Type locality Quitobaquito, Pima Co., Arizona.
Canis microdon Merriam (1897:29). Type locality Mier, on Río Grade, Tamaulipas.
Canis peninsulae Merriam (1897:28). Type locality Santa Anita, Cape Saint Lucas, Baja California.
Canis estor Merriam (1897:31). Type locality Noland's Ranch, San Juan River Valley, San Juan Co., Utah.
Canis vigilis Merriam (1897:33). Type locality near Manzanilla, Colima.
Canis clepticus Elliot (1903:225). Type locality San Pedro Martir Mountains, 2,590 m, Baja California.
Canis impavidus Allen (1903:609). Type locality Río de las Bocas, 2153 m, northwestern Durango.
Canis goldmani Merriam (1904:157). Type locality San Vicente, Chiapas.
Canis jamesi Townsend (1912:130). Type locality Tiburon Island, Sonora.
Canis hondurensis Goldman (1936:33). Type locality Cerro Guinote, NE of Archaga, on the Talanga road north of Tegucigalpa, Honduras.

CONTEXT AND CONTENT. Order Carnivora, Family Canidae, Genus *Canis*, in which there are eight recognized species. There are 19 recognized subspecies of *C. latrans*, which is considered to be a close relative of the jackals (*C. aureus*, *C. mesomelas*, and *C. adustus*)—see Kurtén, 1974, and Remarks. For more details on subspecies see Nelson (1932), Jackson (1951), and Hall and Kelson (1959).

C. l. latrans Say (*in* James, 1823:168), see above (*pallidus* Merriam and *nebracensis* Merriam are synonyms).
C. l. ochropus Eschscholtz (1829:1), see above.
C. l. cagottis (Hamilton-Smith, 1839:164), see above.
C. l. frustror Woodhouse (1850–51:147), see above.
C. l. lestes Merriam (1897:25), see above.
C. l. mearnsi Merriam (1897:29), see above (*estor* Merriam a synonym).
C. l. microdon Merriam (1897:29), see above.
C. l. peninsulae Merriam (1897:28), see above.
C. l. vigilis Merriam (1897:33), see above.
C. l. clepticus Elliot (1903:225), see above.
C. l. impavidus Allen (1903:609), see above.
C. l. goldmani Merriam (1904:157), see above.
C. l. texensis Bailey (1905:175). Type locality Santa Gertrudis, Kleberg Co., Texas.
C. l. jamesi Townsend (1912:130), see above.
C. l. dickeyi Nelson (1932:224). Type locality near Cerro Mogote, 3.2 km W Río Goascoran, La Unión (13°30′ north latitude), Salvador.
C. l. colatus Hall (1934:369). Type locality Isaacs Lake, Bowron Lake Region, British Columbia.
C. l. hondurensis Goldman (1936:33), see above.
C. l. thamnos Jackson (1949:31). Type locality Basswood Island, Apostle Islands, Ashland Co., Wisconsin.
C. l. umpquensis Jackson (1949:31). Type locality 5 mi. SE Drew, Douglas Co., Oregon.

DIAGNOSIS. The coyote can be differentiated from other *Canis* in the Western Hemisphere (gray wolf, *C. lupus*; red wolf, *C. rufus*; and domestic dog, *C. familiaris*) using a number of criteria. The coyote is typically smaller than the gray wolf (see General Characters and also Mech, 1974), but there is overlap when comparing the coyote with the red wolf and the domestic dog. Also, depending on geographic locale, there may be slight overlap with *C. lupus* (Lawrence and Bossert, 1967). The nose pad of the coyote (approximately 25 mm in diameter) is smaller than that of the wolf as is the diameter of the pad on the hind foot (less than 32 mm as opposed to greater than 38 mm, respectively). The ears of the coyote are longer than those of the gray wolf. The track of the coyote (approximately 70 mm by 60 mm—O. J. Murie, 1954) is more elongated than that of the domestic dog, but shorter than that of both the gray wolf and the red wolf. Riley and McBride (1975) presented mean values of 66 mm (57 to 72 mm) and 102 mm (89 to 127 mm) for the track length (from the back of the heel to the end of the longest claw) for the coyote and red wolf, respectively. The stride of the coyote is less than that of the gray wolf or red wolf. The mean length of the stride of the coyote is approximately 414 mm (324 to 483 mm), whereas that of *C. rufus* is approximately 658 mm (552 to 762 mm; Riley and McBride, 1975).

Dental characters also have been used to distinguish *latrans*, *lupus*, and *rufus*, but Jackson (1951) stressed that such measurements may not be especially reliable. In the coyote, the tips of the upper canine teeth usually extend below a line drawn through the anterior mental foramina of the mandible when the mandible is articulated and the jaws closed. Howard (1949) suggested a way for differentiating *latrans* from *familiaris* that is about 95% reliable, depending on subspecies. A ratio of palatal width (between the inner margins of the alveoli of the upper first molars) to length of the upper molar toothrow (from the anterior margin of the aveolus of the first premolar to the posterior margin of the last molar alveolus) is calculated. If the tooth row 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.

Various cranial measurements have been used to differentiate species of *Canis* (Lawrence and Bossert, 1967, 1969, 1975; Paradiso, 1968; Paradiso and Nowak, 1971; Wortmann, 1971; Gipson *et al.* 1974). The coyote has a relatively larger braincase than does *C. lupus* (Mech, 1974). Paradiso and Nowak did extensive analyses on skulls of *latrans*, *lupus*, and *rufus*, and demonstrated the usefulness of indices. They found no overlap when comparing the largest coyote to the smallest wolf (*lupus*) in zygomatic breadth (greatest distance across zygomata), greatest length of the skull (see figure 1), or bite ratio (the ratio of the width across the outer edges of the alveoli of the anterior lobes of the upper carnassials to the length of the upper molar toothrow, as defined above). *C. rufus* resembles *C. latrans* more than *C. lupus*, but Paradiso and Nowak (1971) regarded *latrans* and *rufus* as sufficiently distinct to warrant specific recognition. The differences between the red wolf and the coyote are far greater than those between recognized subspecies of *C. latrans*. The most reliable feature separating *latrans* from *rufus* is lesser size; there is almost no overlap in greatest length of the skull (figure 1). Also, *rufus* has heavier bone structure, a relatively broader skull, and generally a more pronounced sagittal crest. Lawrence and Bossert (1967), using multiple character analyses and linear discrimination techniques, found nine cranial and six dental measurements (see Lawrence and Bossert, 1967, table 1 and appendix A, for particulars) that could be used reliably to differentiate *latrans* from *lupus* and *familiaris*, but no single character was found without overlap between a pair of species. *C. latrans* differed more from *lupus* and *familiaris* than *lupus* differed from *familiaris*.

The coyote brain differs from that of *C. lupus* (Radinsky, 1973) in that the wolf has a dimple in the middle of the coronal gyrus, whereas the coyote does not. Using gross cerebellar morphology, Atkins and Dillon (1971) distinguished *latrans* from both *lupus* and *rufus* (see Remarks). The coyote differs from *C. lupus* and *C. familiaris* serologically (Leone and Wiens, 1956; but see also Seal, 1975).

Behaviorally, the coyote can be differentiated from *C. lupus* and *C. familiaris*. The coyote shows higher levels of aggression earlier in life than does the wolf or beagle (and probably most

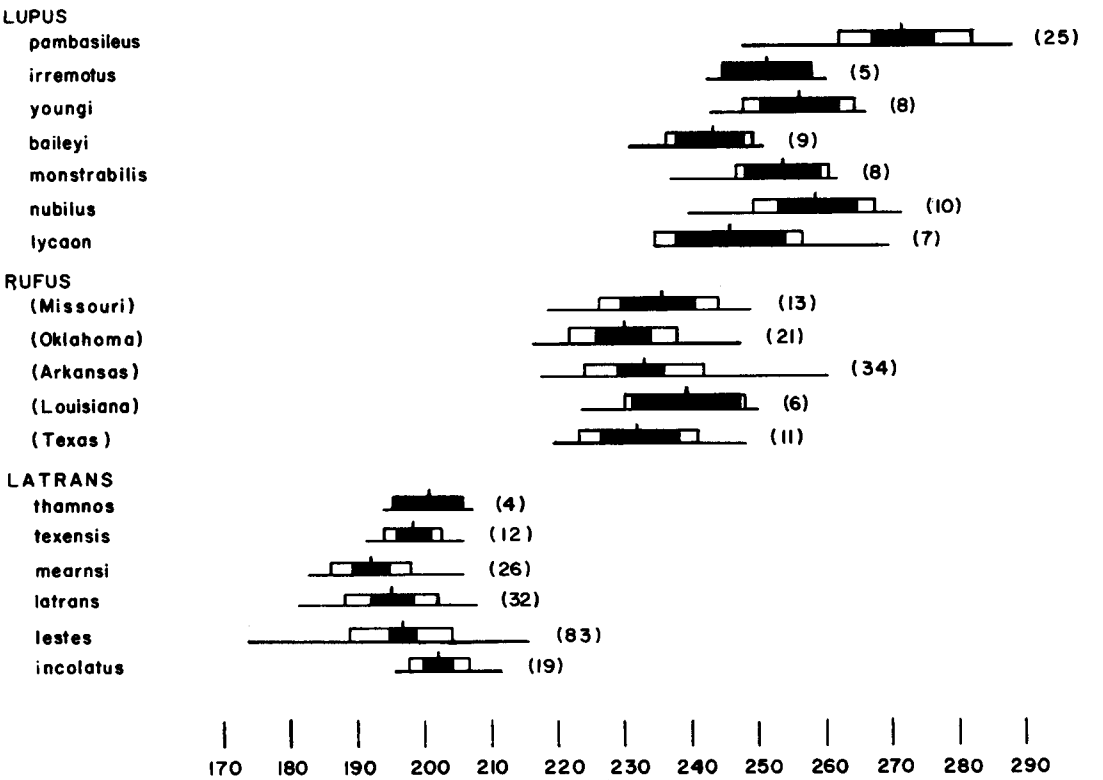

FIGURE 1. The greatest length of skull (mm) in male gray wolves (*lupus*), red wolves (*rufus*), and coyotes (*latrans*). A similar trend also is evident in females (slender line = range; black bar = 2 standard errors of the mean; vertical line on top of black bar = mean; black bar plus white portion on either side indicate one standard deviation on either side of the mean). After Paradiso and Nowak, 1971, with permission.

other domestic dogs as well) and also performs a "species-typical" behavior called the "inguinal response" which consists of rotating a hind-leg outwards or lifting it off the ground in response to light inguinal contact (see figure 2, and Bekoff, 1972*a*, 1973, 1974*a*).

GENERAL CHARACTERS. The size of the coyote varies with subspecies and geographic locale (Jackson, 1951; Hall and Kelson, 1959). Adult males usually are heavier and larger than adult females (approximately 8 to 20 kg as opposed to 7 to 18 kg, respectively). In Sagehen Creek Basin (northeastern California), Hawthorne (1971) found that males averaged 11.12 kg (8.17 to 12.49 kg) and females averaged 9.76 kg (7.72 to 12.03 kg), whereas in Texas Daniel (1973*a*) found that 71 males averaged 16.75 kg (11.35 to 20.43 kg) and 70 females averaged 13.62 kg (10.90 to 17.25 kg). Gier (1975) reported that northern subspecies are larger (approximately 18 kg) than more southern subspecies on the Mexican deserts (11.5 kg). Body length varies from 1.0 to 1.35 m and the tail is about 400 mm long. Females are shorter than males in both length and height. The largest coyote on record was taken in Wyoming. It weighed 33.94 kg and measured 1.60 m from tip of nose to tip of tail (Young, 1951).

Color and texture of the fur vary geographically. The hair is longer and coarser in northern subspecies (see Form). The banded nature of the hair presents blended colors—gray mixed with a reddish tint. Those coyotes at higher altitudes tend toward more gray and black, whereas those in the desert are more fulvous (Jackson, 1951). Black patches may be found on the front of the forefeet and near the base and tip of the tail (Gier, 1968). The belly and throat are paler than the rest of the body. Melanistic coyotes are rare (Young, 1951; van Wormer, 1964; Gipson, 1976).

DISTRIBUTION. Coyotes are Nearactic canids originally inhabiting open country and grasslands (Young, 1951; Gier, 1975). Within historic time, they have occupied many diverse habitats. They now can be found between 10° north latitude (Costa Rica) and 70° north latitude (northern Alaska) and throughout the continental United States and Canada (fig. 3). The range of the coyote is expanding. When considering the expanding range of *C. latrans* it is important to know whether this reflects true movement of coyotes or whether some recently discovered populations (in some cases a few dens) are the result of animals being transplanted into the region by man. Transplantation appears to have occurred into Florida (Cunningham and Dunford, 1970) and Georgia (Fisher, 1975). Paradiso (1968) considered the expansion of the coyote into Arkansas, Mississippi, and Louisiana to have been unassisted by humans.

FOSSIL RECORD. Fossils resembling *C. latrans* were found in Pleistocene deposits in Cumberland Cave, Maryland (Gidley, 1913; Matthew, 1930). Differentiation of modern canids occurred in the Pleistocene and in Recent times (see Giles, 1960; Colbert, 1969; Todd, 1970).

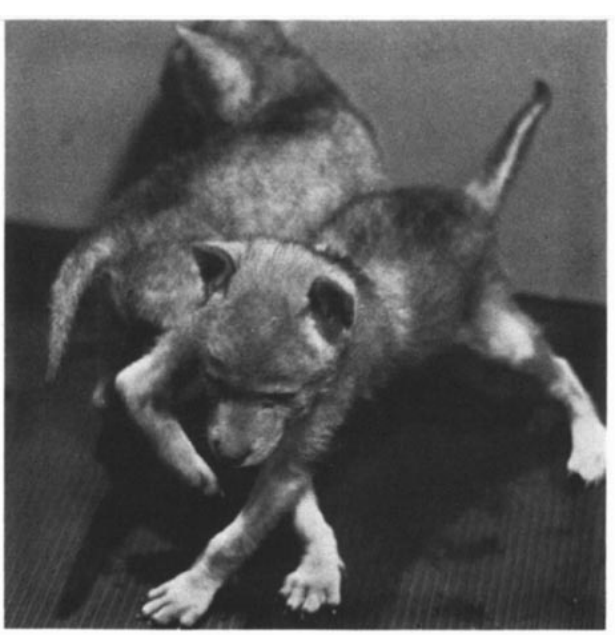

FIGURE 2. A "species-typical" action, the inguinal response, performed by the coyote on the left. The leg is not being pushed up but is lifted due to light stimulation in the inquinal region.

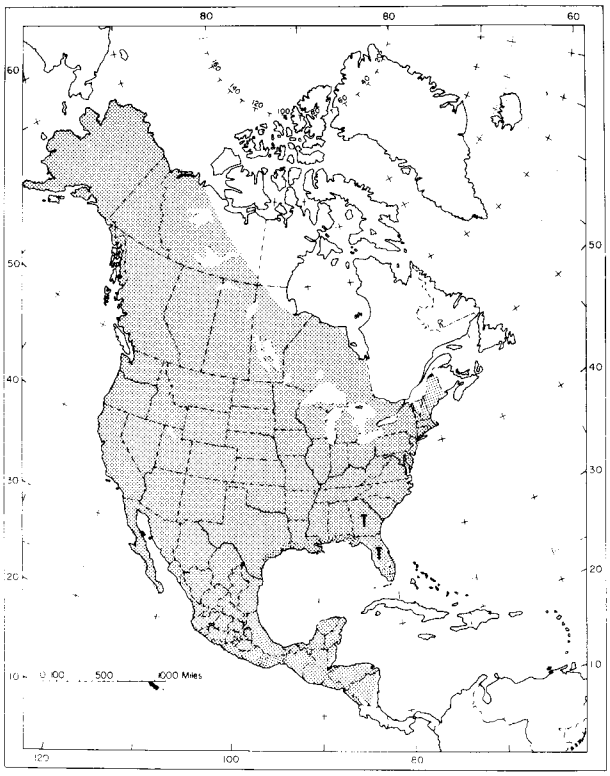

FIGURE 3. Current distribution of coyote (T, probable transplants by man—see text).

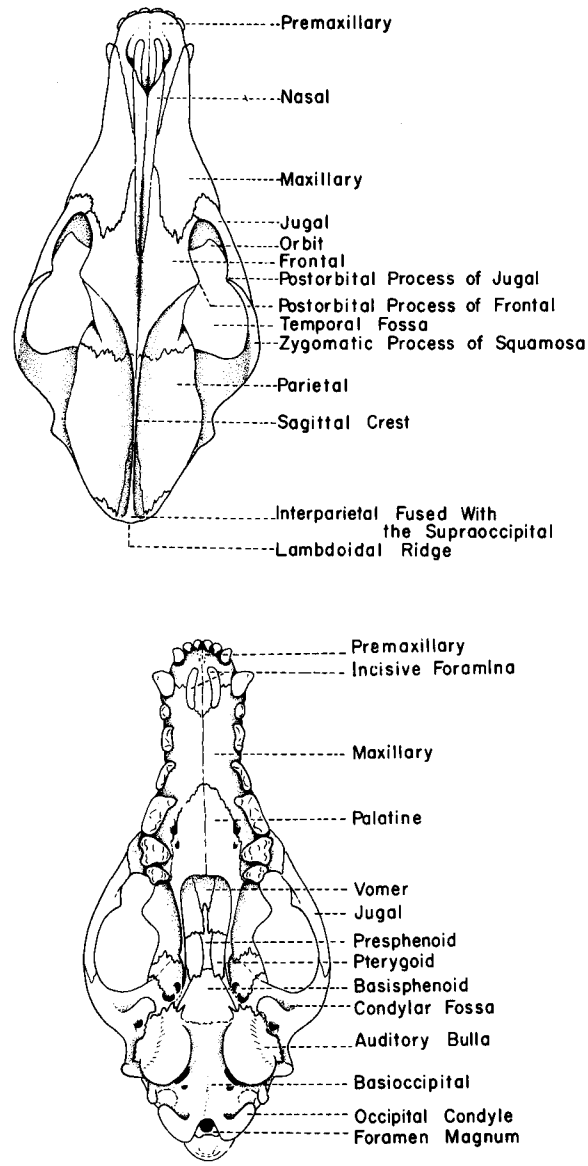

FIGURE 4. Skull of coyote: upper left, dorsal view; lower left, ventral view (from Lechleitner, 1969, with permission of the publisher).

FORM. Coarse guard hairs are about 50 to 90 mm long (in the mane, 80 to 110 mm) with imbricate scales that are acuminate in the proximal region, crenate medially, and flattened distally. The fine underfur has coronal scales and may be as long as 50 mm (see Adorjan and Kolenosky, 1969; Ogle and Farris, 1973). There usually is one main molt between late spring and autumn, the summer coat (both guard hairs and underfur) is shorter than the winter coat. About 50 mm down from the base of the tail there is an oval tail gland (10 by 3 mm; Hildebrand, 1952). Normally there are eight mammae. The front foot has five toes and the hindfoot four. On the front foot there is a dew claw proximal from the other four toes. P. S. Gipson (personal communication) observed a specimen with a well-developed dew claw on each hindfoot. The toes are nonretractile and the stance digitigrade. There are 42 teeth (i 3/3, c 1/1, p 4/4, m 2/3; for further details on dentition see Slaughter *et al.*, 1974, and Bekoff and Jamieson, 1975). The skull of a mature male weighs between 170 and 210 g and is 180 to 205 mm long (figures 4 and 5) from the tip of the premaxilla to the posterior rim of the coronal crest (Gier, 1968). Males show greater development of the sagittal ridge than do the females.

The structure and evolution of the coyote's brain have been described by Radinsky (1969, 1973), Atkins and Dillon (1971), and Elias and Schwartz (1971).

Mossman and Duke (1973) described the ovaries of various canids. The adrenals of canids were studied by Ogle (1971) and Heinrich (1972). Ogle (1971) reported that the left adrenal is heavier than the right in both males and females and that the adrenals of females tend to be heavier than those of males (1.14 ± 0.01 as opposed to 1.08 ± 0.03 g, respectively).

FUNCTION. The coyote's fur is similar in insulative value to that of the gray wolf (Ogle and Farris, 1973). The critical temperature of *latrans* is -10°C (O_2 consumption = 7.35 $mm^3/g/min$; Shield, 1972). The longer winter fur coat conserves heat considerably better than the shorter summer coat, there being a decrease of about 87% in thermal conductivity and an increase in insulative value by a factor of five (for details, see Ogle and Farris, 1973). The coyote can run as fast as 48 km/hr (Sooter, 1943) but usually trots at less than 32 km/hr. Coyotes, like other canids (Kleiman, 1966; Mech, 1974) appear to use olfactory cues during their activities and deposit "marks" (urine, feces, and possibly glandular secretions) on conspicuous objects, possibly for territory demarcation (as yet an unsubstantiated assumption). Ozoga and Harger (1966) reported that the coyotes they observed urinated an average of once per 4.0 km and defecated every 10.4 km. Gipson and Sealander (1972) reported urination and defecation occurring three times per 1.6 km and one time per 3.2 to 4.8 km, respectively. Scratching of the ground is also a common component of the eliminative process in canids and it is possible that scent from interdigital glands is thus deposited.

The coyote has an elaborate vocal repertoire (Tembrock, 1963; Lehner, 1975). The region of maximal sensitivity to auditory stimuli is 100 Hz to 30 kHz with a top limit of 80 kHz (Petersen *et al.*, 1969). The retina is duplex and has a preponderance of rods. The absolute scotopic (rod) threshold is approximately 1.4 foot-candles. The adaptation curve shows distinct rod-cone breaks (Horn and Lehner, 1975). The electrocardiograph of the coyote based on the ventricular activation process is the same as of other carnivores (Szabuniewicz, 1970).

REPRODUCTION AND ONTOGENY. Field data on courtship in coyotes and other species of *Canis* are scanty. Data on captive animals (Bekoff and Diamond, 1976) indicate that courtship may begin as long as 2 to 3 months before there are attempts at copulation. The female is monoestrous, showing one period of "heat" per year. This usually occurs between January and March, and both males and females show seasonal changes and cycles in reproductive anatomy and physiology (Hamlett, 1938; Gier, 1968; Kennelly, 1972; Dunbar, 1973).

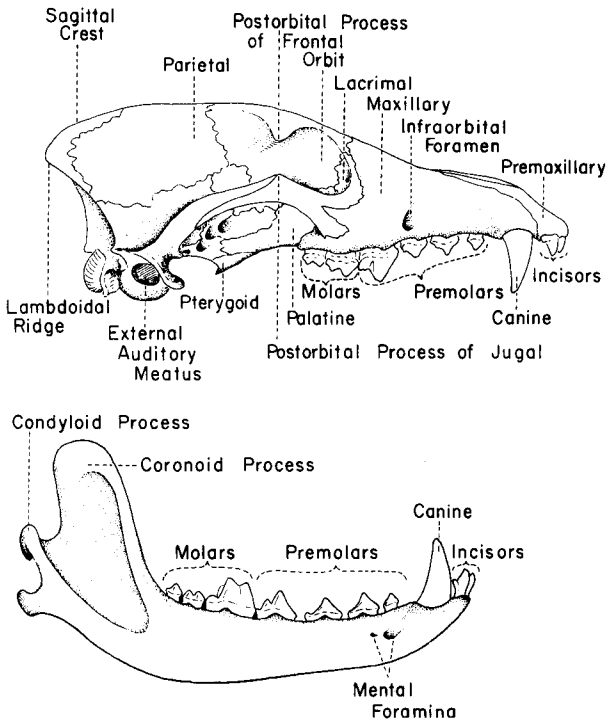

FIGURE 5. Skull and jaw of coyote in lateral view (from Lechleitner, 1969, with permission of publisher).

Proestrous lasts between 2 and 3 months (Whiteman, 1949; Kennelly and Roberts, 1969; Bekoff and Diamond, 1976), estrus lasts about 2 to 5 days (Kleiman, 1968; personal observations), and ovulation occurs about 2 to 3 days before the end of the female receptivity. The times of, and durations of, proestrous and estrous differ in various locales and the relationship is not clear-cut (Hamlett, 1938). The same is true for the spermatogenic cycle of the male. Behavioral changes that occur during courtship parallel those reported by Golani and Mendelssohn (1971) for the golden jackal (*C. aureus*). Courtship "rituals" are not so highly specific that hybridization cannot occur. Coyotes can successfully mate with domestic dogs, gray wolves, red wolves, and jackals. Copulation ends with the typical "copulatory tie," during which the male's penis is locked in the female's vagina (Dewsbury, 1972; Grandage, 1972; Fox and Bekoff, 1975). The tie can last 15 to 25 minutes (Kleiman, 1968; Bekoff and Diamond, 1976). It is generally accepted that the same individuals will mate from year to year, but not necessarily for life.

The percentage of females that breed during a given year may vary from 33% to 90% depending on local conditions (Gier, 1968; Knowlton, 1972; Gipson *et al.*, 1975). Both yearling males and females are capable of reproducing, yearling females usually breeding later than older females (Gier, 1968) and thus contributing minimally to the population (Knowlton, 1972). Gipson *et al.* (1975) found that no yearling females bred. However, (Gier, 1968) reported that in good rodent years, 75% of yearling females may breed. Nellis and Keith (1976) reported pregnancy rates of 94% for adult females and 14% for yearlings, with adults showing more (6.0) placental scars than yearlings (5.2)—not a significant difference). Asdell (1964), summarizing the literature, reported the mean number of embryos in 1370 cases to be 6.23 and the number of den young in 1582 cases to be 5.70. Hamlett (1938) reported that the number of young per litter was about 85% of the number of embryos per female. Gier (1975) estimated that the number of young born was equal to about 80% of the ovulated ova depending on whether or not it was a good rodent year. Gipson *et al.* (1975) reported the mean number of ova per breeding female to be 6.2, with 4.5 becoming implanted.

Gestation lasts approximately 63 days (58 to 65). Coyotes and dogs appear to develop similarly *in utero* (Gier, 1968). Average litter size is six with a sex ratio of females to males of about 1:1. Nellis and Keith (1976) reported a mean litter size of 5.3 for 26 litters. Litter size is known to be accepted by population density (Knowlton, 1972) and rodent populations (Gier, 1968). Litter size averaged 4.3 at high densities and 6.9 at low densities. In good rodent years mean litter size was 5.8 to 6.2 and in poorer rodent years average litter size was 4.4 to 5.1.

TABLE 1. Mortality in coyote populations. (After Mathwig, 1973: 184; mean percentage values based on seven studies).

Age (years)	Percent of population
1	41.1
2	19.1
3	11.0
4	6.6
5	6.6
7	3.7
8	2.7
9	2.1
10	1.3
11	0.3
12	0.9

Young are born blind and helpless, usually in an excavated den. Favorable den sites include brush covered slopes, steep banks, thickets, hollow logs, rock ledges, often on south-facing slopes (Gier, 1968). Dens of other animals may be used. Dens are usually about 0.3 m in diameter and may be from 1.5 to 7.5 m long (van Wormer, 1964). More than one entrance may facilitate the movement of young when the den site is disturbed. The same den may be used from year to year, and dens may be shared. Nellis and Keith (1976) found that 3 of 29 dens had two litters.

Young are nursed by their mother (see Ewer, 1973:331, for data on the composition of coyote milk) and are weaned at about week 5 to 7 (Snow, 1967; unpublished data). They begin to eat solid food at about week 3, and the female (and possibly the male) begins regurgitating semi-solid food at this time. The male apparently plays some role in rearing the young by bringing food to the lactating bitch and the pups. Pregnant and lactating females require about 900 g, or 1.5 times the "normal" amount, of food per day (Gier, 1975). Weight at birth is about 250 to 275 g and length of the body (tip of head to base of tail) is about 160 mm (Gier, 1968; Bekoff and Jamieson, 1975). Between birth and week 8 the average weight increase is about 0.31 kg/week (Bekoff and Jamieson, 1975), and the pups reach adult weight at about month 9. Eyes open at about day 14. Teeth erupt as follows (on the average): 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 without maternal assistance by week 2 or 3. Jackson (1951) described the sequence of the closing of cranial sutures.

Young emerge from the den in week 2 or 3 and may disperse in months 6 to 9. Not all young disperse. Although there are no field data, consistent reports on the development of social behavior in captive coyotes (Fox and Clark, 1971; Bekoff, 1972*a*, 1974*a*, 1975*a*) indicate that young coyotes form dominance relationship via severe, unritualized fights between 25 and 35 days of age.

Coyotes in captivity may live as long as 18 years (Young, 1951) but in wild populations few individuals live more than 6 to 8 years (Gier, 1968; Mathwig, 1973). Maximum ages known in the wild are 13.5 (Nellis and Keith, 1976) and 14.5 years (Knowlton, 1972). In an unexploited population, Knowlton (1972) found 70% of individuals in spring (pre-whelping) to be less than 3 years old and less than 5% to be more than 9 years old. In autumn, more than 80% of the individuals were less than 3 years old. Knowlton reported a 40% annual mortality rate for coyotes more than a year of age, with relatively high survival between years 4 and 8. Estimated mortality rates in central Alberta (Nellis and Keith, 1976) were 71% through year 1 and 36% to 42% for animals more than a year old (see table 1). In Iowa, Mathwig (1973) found greatest life expectancy at 1½ years and least at 5½. To maintain stability, a net survival of 33% was needed in the populations that Knowlton (1972) studied, whereas Nellis and Keith calculated that 38% survival was necessary. Gier (1968) felt that there were three basic limits on reproduction: 1) climatic factors, 2) parasites and disease, and 3) food. Losses due to predation, accidents, and man are also important.

ECOLOGY. More is known about the ecology of the coyote than perhaps any other carnivore (see Bekoff, 1974*b*). Many data have been collected because of the economic interests of control and management programs. The coyote is an opportunistic predator and includes a wide variety of food in its diet, the percentage by volume and weight varying individually and also with season and locality. Korschgen (1957) listed 56 animal, 28 plant, and six miscellaneous food items in Missouri and A. Murie (1940) and Mathwig (1973) and others have included large numbers of plant species. Individuals in captivity (Gier, 1975) require about 600 g of meat per day.

FIGURE 6. Aggressive displays by two 23-day-old coyotes.

TABLE 2. Data on coyote movements from eight representative studies (distances in km).

Study	Adult		Juvenile		
	Males	Females	Males	Females	Both sexes
Garlough, 1940					42.9
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	
Chesness, 1972	10.1		6.4	6.6	
Gipson and Sealander, 1972	20.5	8.16		7.4	
Nellis, 1975	6	7	6	26	

Because of the varied diet, it is impossible to list all food items that have been found in scats and stomachs or observed being taken in actual kills. Deer, elk, sheep, rabbits, various rodents, ground-nesting birds such as the ferruginous hawk (Angell, 1969), bobwhite quail (Lehmann, 1946), and Canada geese (Vermeer, 1971), amphibians (Minckley, 1966), lizards, snails, fish, crustaceans, and insects comprise the "meat" items. Various berries, peaches, pears, apples, persimmons, watermelons, cantaloupes, and carrots are included in the vegetables, and leather boots, tin cans and the like are included in the miscellaneous list. Overall, about 90% of their diet is mammalian flesh.

In the winter, much of the coyote's diet is made up of the carrion of large game animals such as deer (see Sperry, 1933, who reviewed data for 10 western states; O. J. Murie, 1935; A. Murie, 1940; Ozoga and Harger, 1966; Gier, 1968; Ogle, 1971; Mathwig, 1973; Nellis and Keith, 1976) and little vegetable food is eaten. In the spring, summer, and autumn there is an increase in the percentage (by volume and weight) of various rodents (A. Murie, 1940; Nellis and Keith, 1976). Fichter *et al.* (1955) noted that a striking seasonal trend in Nebraska was an autumnal increase in the utilization of fruit. Gipson (1974) summarized five studies on the food habits of coyotes in their original range and the compiled percentage data were as follows: rabbits, 41.1; rodents, 36.2; carrion, 25.5; livestock, 21.9; wild birds, 15.0; deer, 7.9; fruits, 6.7; and poultry, 4.8. Most analyses of coyote predation on both large game mammals and domestic livestock indicate that young, old, and sick animals constitute the bulk of this portion of their diet (A. Murie, 1944; Ozoga and Harger, 1966; Knowlton, 1968; Cook, White, Trainer, and Glazener, 1971; Ogle, 1971; Hawthorne, 1972; Davenport, Bowns, and Workman, 1973), and that coyote predation was not a primary limiting factor on game and livestock. A. Murie (1935) found that 70.29% of the coyote's diet in Jackson Hole, Wyoming, was "beneficial" to the prey, 18.22% was "neutral," and only 11.49% was "harmful." Similarly, Mathwig (1973) found that 85% of the coyote's diet in Iowa was not "harmful," whereas 15% was "detrimental." Ozoga and Harger (1966) reported that healthy deer could escape from coyotes and bighorn sheep are able to chase off coyotes (Weaver and Mensch, 1970). Davenport *et al.* (1973) indicated that most lambs lost during spring died from causes other than predation, such as starvation, disease, abandonment, docking, and infection. Daniel (1973*b*) wrote ". . . although fawn survival rates most probably are closely related to coyote numbers and predation, there are other factors of perhaps *more importance* [my emphasis] exhibiting strong influence upon the growth and stability of deer herds. . . ." There is little evidence that coyote predation is a primary limiting factor on populations of big game or domestic livestock.

Ozoga and Harger (1966) wrote that the average chase of a deer by a coyote was about 55 m and they observed two long futile attempts of 4.32 and 4.64 km by single coyotes. Coyotes will hunt in pairs or in larger groups (Cahalane, 1947; Dobie, 1961; Young, 1951; Ozoga and Harger, 1966; Gier, 1968) and will form hunting relationships with other predators such as golden eagles (Engel, 1966), ravens (A. Murie, 1940), and badgers (Dobie, 1951). Actual coyote attacks are rarely observed and little is known about their predatory habits (White, 1973). A presumed "coyote kill" often has been killed by some other predator, sometimes a domestic dog (Davenport *et al.*, 1973). Ogle (1971) listed five criteria that can be used to distinguish deer killed by coyotes from those fed on as carrion. Coyote kills may be characterized by: 1) large patches of hide leading to the carcass; 2) separation of vertebral column in the thoracolumbar region of adults and at the atlas of fawns; 3) nasal and maxillary bones chewed away; 4) ribs, vertebrae, and scapulae chewed; and 5) limbs widely scattered. For adult deer, the first criterion is considered to be the most reliable. Attacks on the head and neck frequently are used on deer (Ozoga and Harger, 1966; White, 1973) as are belly and rump attacks (Ogle, 1971). A shearing bite is used (Young, 1951), and a bite-and-tear sequence is common. For smaller mammals a stalk-and-pounce approach is common. Coyotes generally eat the contents of the stomach and intestines of young but not of adults (Davenport *et al.*, 1973; White, 1973). See Bekoff (1975*a*, 1975*b*) for information on the development of predatory behavior in coyote pups.

Coyotes carry a wide variety of parasites (Young, 1951; Gier, 1968; Thornton, Bell, and Reardon, 1974). Fleas are the most common external parasite—*e.g. Pulex similan*, *Hoploxpsyllas affinis* and *Cediopsylla simplex* (rabbit flea), *Chaeyopsylla lotoris* (raccoon flea), and *Juxtapulex porcinus* (javelina flea). Other external parasites include various ticks (*Ioxedes simulans*, *I. kingi*, and *Dermacentor variabilis*) and lice (*Demidectes*). Internal parasites include the cestodes *Taenia pisiformis* (common according to Gier, 1968) and *Mesocestoides corti*; roundworms, *Physaloptera rara* and *Filaroides osteri* (in the trachea, bronchi, and rarely in the lungs); intestinal worms such as *Toxascaris leonina*; dog hookworms, *Ancyclostoma caninum*, that can pass through the placenta; whipworms, *Trichuris vulpis*; heartworms, *Dirofilaria immitis*; pinworms, Oxyuridae; thornyheaded worms, *Oncicola canis* and *Spriocerca lupi*, in the esophagus, stomach, and aorta; and coccidia fungus, *Isospora rivolta*. Coyotes also have been found to carry tularemia (Kunkel, 1930; Lundgren *et al.*, 1957), distemper (Harispe and Wainer, 1941), rabies (Swick, 1972; Behymer *et al.*, 1974; and others), and bubonic plague (A. M. Barnes, personal communication). In addition, coyotes suffer from dental anomalies (Nellis, 1972), mange (A. Murie, 1944; Holmes and Podesta, 1968), cancer (Trainer *et al.*, 1968; Dietrich and van Pelt, 1972), Q fever (Enright *et al.*, 1971), aortic aneurysms (Thornton *et al.*, 1974), various cardiovascular disorders (Ross and Suzuki, 1973), and serious wounds (for example, bullet wounds), missing limbs, and broken bones.

Coyotes and other carnivores can live in the same area, but coyotes, like other smaller predators, do not compete well with the wolf (Mech, 1966, 1974). Coyotes generally do not tolerate foxes or bobcats (Young, 1951) and puma will kill and eat coyotes (Young, 1946).

Coyotes spend a good deal of time on the move. They are active primarily in early evening, especially in winter (Ozoga and Harger, 1966; Chesness, 1972), but do show sporadic activity in the daylight hours. Gipson and Sealander (1972) showed a principal activity peak at sunset with a minor peak at daybreak in Arkansas. In summer, they found animals to be more active by day, with pups more active by day than adults. Coyote movement patterns have been studied in various places and like the movement patterns of wolves (Mech, 1974), they can be classified as travels within a "territory" or home range, as dispersals, or as long migrations. Males tend to have larger home ranges than do females. In Minnesota, Chesness and Bremicker (1974) found home ranges of males to average 41.92 km^2, whereas those of females averaged 10.08 km^2. Furthermore, the home ranges of the males overlapped considerably but those of the females did not (an implication, but not proof, of ter-

ritoriality). In Arkansas, Gipson and Sealander (1972) reported male home ranges from 20.8 to 41.6 km² and female home ranges from 8 to 9.6 km². Other studies have reported home ranges of 20.8 to 32 km² (Nellis and Keith, 1976), 57.6 to 80 km² (Ozoga and Harger, 1966) and 9.6 to 12.8 km² (Camenzind, 1974). In Minnesota, home ranges were elongate with mean length about 1.8 times mean width.

Many data have been collected concerning length of movements of marked individuals in various locales (table 2). No consistent differences between sexes have been seen. Coyote movements of over 160 km are not uncommon. Ozoga and Harger (1966) found average daily travel to be about 4.0 km.

Movements of young coyotes also have been studied (table 2). Dispersal usually occurs in autumn and winter (October to February), some pups not dispersing during their first year. Dispersal occurs randomly in all directions. Pups will move upwards of 80 to 160 km. Unfortunately, few pups marked at dens are relocated by investigators (22% by Nellis and Keith, 1976).

The density of coyote populations varies with local conditions. Knowlton (1972) suggested that a density of 0.2 to 0.4/km² (0.5 to 1.0/mi²) would be a realistic educated guess for densities over a large portion of the range, and his suggestion fits well with data collected by others (Young, 1951; Ozoga and Harger, 1966; Gier, 1968; Mathwig, 1973; and Nellis and Keith, 1976).

Coyotes are usually observed as lone individuals (Ozoga, 1963; Ozoga and Harger, 1966; Chesness, 1972) or as pairs (especially during the breeding season). Larger groups of coyotes are probably parent(s) and young. "Packs" of coyotes have been described in the literature (Dobie, 1961; Camenzind, 1974), but whether or not they operate as do wolf packs is as yet unknown.

The relationship of the coyote with early man was one of harmony and mutual respect (Dobie, 1961; Gill, 1970). Within the last 150 years this relationship has changed considerably, particularly because of the coyote's predatory habits. In fact, in a recent paper by Shelton (1973), the coyote was referred to as being a "dispensable animal." Indeed, the coyote has been responsible for large economic losses to the domestic livestock industry (Young, 1951; Gier, 1968; Cummings, 1972; Neese, 1973). One of the first bounties on coyotes was established in Missouri in 1825 (Young, 1951). In the 1860's, when beaver decreased in value, the value of coyote rose to about $.75 to $1.50 per animal (for more detail on prices see Young, 1951, and van Wormer, 1964). Coyote fur is not in great demand (Frye and Lay, 1942, ranked it sixth out of seven skins) and Young (1951:118) felt that the use of coyote skins and the success of the bounty system depended on the "fickle dictates of fashion." The bounty system has not been effective (Howard, 1973) and has been supplemented by use of various other control methods such as shooting from snowmobiles (Wetmore *et al.*, 1970) and airplanes, trapping (see Casto and Presnall, 1944, for a comparison of various trapping methods), coyote-getters (M-44 cyanide gun, a selective method—see Beason, 1974), aversive conditioning (Gustavson *et al.*, 1974; Bekoff, 1975*c*), and the use of various chemicals such as strychnine, 1080 (sodium monofluoroacetate, considered by some to be the "best poison"—Howard, 1973), and antifertility agents (diethystilbestrol—Balser, 1964; Kennelly, 1969). Dose regulation and distribution have been problems. Linhart and Kennelly (1967), developed a "marker" (demethychlortetracycline) to "label" animals taking various baits. The efficiency of removing animals that have actually preyed on the items reported damaged is also an important consideration (Gipson, 1975). Knowlton (1972) suggested that control programs should consider the removal of particular individuals from populations. Another control method that has worked to reduce loss of domestic livestock simply involved the removal of carrion by farmers in central Alberta, because coyotes do depend heavily on carrion as part of their winter diet (Todd and Keith, undated). Gier (1968:23) wrote that "coyotes may be encouraged or even taught to kill poultry and other farm animals by farmers discarding dead animals where coyotes can find them." Hunter-trapper programs appear to be the most successful (Howard, 1973; Gier, 1975). However, it is important to realize that few control programs have been effective.

The lack of success of coyote control programs basically is due to the lack of objective studies on the biology of the coyote and other predators (see Hornocker, 1972, and Howard, 1973). Little is known about population dynamics and predatory methods. In addition, ranchers and environmentalists appear equally reluctant to discuss issues (Buys, undated). Howard (1973:3) summed up the problem well: "The ecological role of predators, that of the coyote for example, seldom gets rational consideration, and unproven concepts are often perpetuated rather than challenged scientifically." The lack of patience by those persons suffering economic losses is understandable, however, it might prove beneficial in the end to stop using ineffective methods and harness both time and energy to more efficient, scientifically based programs (Pringle, 1975). Otherwise, indiscriminate attempts at population suppression may once again be resorted to.

Wild coyotes have been studied primarily using radiotelemetry and capture-recapture methods. Both these techniques provide information on movements. Food habits are inferred from scat and stomach analyses and infrequently studied by direct observation. The use of trapping along with other methods provides information on age, sex, weight, size, and breeding condition, and allows blood samples to be drawn. Intramuscular injections of 25 mg of phencyclidine hydrochloride + 25 mg of promazine hydrochloride have been used to immobilize trapped animals (Chesness, 1972). Censusing is frequently done by "siren inventories and trapping." Ages of coyotes may be estimated by counting dental cementum annuli (Linhart and Knowlton, 1967). Utsler (1974) recently suggested alternate methods (eye lens, weight of the baculum, and thermal contraction of tail tendons) that appear to be as accurate as the counting of cementum annuli, and less expensive and less elaborate.

BEHAVIOR. Because of the elusive nature of the coyote, there have been few direct observations of social behavior(s). Detailed studies of behavior other than those dealing with territorial or home range movements have been done on captive animals (Fox, 1970; Fox and Clark, 1971; Bekoff, 1972*a*, 1972*b*, 1974*a*, 1975*a*; Brown, 1973). Field observations indicate that the coyote is less social than either the gray wolf of the red wolf (Riley and McBride, 1975), although large "packs" of coyotes have been observed. Gier (1975) wrote that there is no known social structure other than the family. Young coyotes form dominance relations via severe fights between 25 and 35 days of age (figure 6; Fox and Clark, 1971; Bekoff, 1972*a*, 1974*a*). The relationship between early fighting and later social organization is not clear, but there are rank-related behaviors that may play some role. For example, higher ranking animals are less successful at getting littermates to play with them and spend less time interacting with them (Bekoff, 1977*a*). These animals also tend to remain at a greater distance from littermates and frequently are asynchronous in activity with the rest of the group. Such higher ranking individuals may be those who later leave the group. In addition, is has also been found (unpublished data) that the lowest ranking member of a litter interacts infrequently with littermates and perhaps such individual(s) would also leave the group. Field testing of these hypotheses is underway. During agonistic interactions, dominant pups and adults approach one another with a stiff-legged gait, ears forward and erect, fur on the back erect (piloerection), the tail at about a 45° angle from the vertical, and frequently snarling and exposing the teeth by vertically retracting the lips. Submission may take the form of flight, active avoidance, or passive or active submission (see Schenkel, 1967, for detailed descriptions). During passive submission the animal rolls over on its back, flattens its ears against its head, usually retracts the lips horizontally into a "submissive grin," and may urinate and whine. During active submission the animal approaches its "partner" in a low crouch-walk with the tail either tucked or held low, and may perform face-licking and face-pawing. Active submission probably develops from food-begging and passive submission appears to have developed from the posture that the pups assume when they are stimulated to excrete by their mother or other adults (Schenkel, 1967). There are large increases in aggression at the time that the female comes into heat. Detailed studies of social play behavior have been reported by Bekoff (1974*a*, 1975*d*).

During early stages of courtship, the male becomes increasingly attracted to the female's urine or feces, or both (Bekoff and Diamond, 1976). See Reproduction and Ontogeny for more detail. When the female is ready to copulate she will tolerate mounting attempts by the male and will flag her tail to one side. After "tieing" the male steps over the back of the female and the couple remain locked at 180° for periods of 5 to 25 minutes.

Coyotes use visual, auditory, olfactory, and probably tactile signals for communication purposes. Alcorn (1946) recognized three distinct calls (squeak, howl call, and distress call). Lehner (1975), through extensive analyses of coyote vocalizations, detailed 11 graded signals. Vocally, the coyote is much like the jackal (Tembrock, 1963). Visual signals such as postures, gestures, and facial expressions have also been described (Fox, 1970, 1975*a*; Bekoff, 1972*a*, 1972*b*, 1974*a*). The coyote appears to have a more elaborate repertoire of visual signals than do more solitary canids such as the red fox, *Vulpes vulpes*, but a less elaborate repertoire than does the wolf (Fox, 1975*a*). Coyotes do deposit scent but the use of this for territorial demarcation and identification has not been proven (see Kleiman, 1966, for alternative hypotheses). During social investigation there is considerable sniffing of various regions of the body. Whether or not scent is deposited from interdigital glands is not known.

GENETICS. The coyote has 39 pairs of chromosomes (Wurster and Benirschke, 1968). The autosomes are acrocentric or telocentric and the sex chromosomes are submetacentric (Hsu and Benirschke, 1967, cited by Mech, 1974). Fertile hybrids have been produced by crossing coyotes with domestic dogs (Young, 1951; Kennelly and Roberts, 1969; Silver and Silver, 1969; Mengel, 1971), with wolves (*rufus* and *lupus*—Young, 1951; Kolenosky, 1971; Paradiso and Nowak, 1971; Riley and McBride, 1975), and with the jackal (Seitz, 1965). Coyote-dog hybrids show decreased fecundity (Mengel, 1971; Gipson *et al.*, 1976). See Riley and McBride, 1975, for detailed comparisons of external characteristics of red wolves, coyotes, and hybrids.

There has been considerable controversy about the "New England canid" (see Lawrence and Bossert, 1969, 1975; Silver and Silver, 1969; Richens and Hugie, 1974). This canid differs from known coyote-dog hybrids and has incorrectly been referred to as a coy-dog. The general concensus is that the New England canid is an extreme expression of a trend already present in *C. l. thamnos* and cranial evidence (Lawrence and Bossert, 1969) and data from behavioral development (Bekoff *et al.*, 1975) suggests that New England canids predominantly are coyotes with some introgression of dog and wolf genes.

REMARKS. The word "coyote" means "barking dog" and is taken from the Aztec word "Coyotyl."

The coyote resembles jackals in many respects and Atkins and Dillon (1971) have grouped *C. latrans* with *C. mesomelas* (black-backed jackal) and *C. aureus* (golden jackal) based on cerebellar morphology.

During its movements, the coyote may function as a seed-carrier (Young, 1951). Kleiman and Eisenberg (1973) made detailed comparisons of canids and felids and Fox (1975*b*) edited a volume dealing with wild canids. A fairly comprehensive bibliography has been compiled (Bekoff, 1974*b*) and Knowlton (1974) also assembled a useful list of references. Volume 3 of the *Coyote Research Newsletter* contains abstracts of papers presented at a National Coyote Workshop (Denver, Colorado, November 1974). Many aspects of coyote biology will be dealt with in a forthcoming volume (Bekoff, 1977*b*).

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