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Modern range of *Canis latrans*

## Physical description

Coyote males average 8–20 kg (18–44 lb) in weight, while females average 7–18 kg (15–40 lb), though size varies geographically. Northern subspecies, which average 18 kg (40 lb), tend to grow larger than the southern subspecies of Mexico, which average 11.5 kg (25 lb). Body length ranges on average from 1 to 1.35 metres (3 ft 3.37 in to 4 ft 5.15 in), and tail length 40 centimetres (16 in), with females being shorter in both body length and height.<sup>[16]</sup> The largest coyote on record was a male killed near Afton, Wyoming on November 19, 1937 which measured 1.6 metres (5 ft 3 in) from nose to tail, and weighed 33.9 kilograms (75 lb).<sup>[17]</sup> Scent glands are located at the upper side of the base of the tail and are a bluish black color.<sup>[18]</sup>

The color and texture of the coyote's fur varies somewhat geographically.<sup>[16]</sup> The hair's predominant color is

light gray and red or fulvous, interspersed around the body with black and white. Coyotes living on high elevations tend to have more black and gray shades than their desert-dwelling counterparts, which are more fulvous or whitish-gray.<sup>[19]</sup> The coyote's fur consists of short, soft underfur and long, coarse guard hairs. The fur of northern subspecies is longer and denser than in southern forms, with the fur of some Mexican and Central American forms being almost hispid.<sup>[20]</sup> Albinism is extremely rare in coyotes; out of a total of 750,000 coyotes harvested by Federal and cooperative hunters between March 22, 1938 to June 30, 1945, only two were albinos.<sup>[19]</sup>



Life study by Ernest Thompson Seton (1886).

The coyote is typically smaller than the gray wolf, but has longer ears and a larger braincase,<sup>[16]</sup> as well as a thinner frame, face and muzzle.

The coyote also carries its tail downwards when running or walking, rather than horizontally as the wolf does.<sup>[21]</sup> Coyote tracks can be distinguished from those of dogs by their more elongated, less rounded shape.<sup>[22]</sup> Scent glands are smaller than the gray wolf's, but the same color.<sup>[18]</sup> Its fur color variation is much less varied than that of a wolf.

## History

By the time of the European colonization of the Americas, coyotes were largely confined to open plains and arid regions of the western half of the continent.<sup>[23]</sup> It is often difficult in early post-Columbian historical records to distinguish between coyotes and wolves. One record from 1750 in Kaskaskia, Illinois written by a local priest noted that the "wolves" encountered there were smaller and less daring than European wolves. Another account from the early 1800s in Edwards County mentioned wolves howling at night, though these were likely coyotes.<sup>[24]</sup> The species was encountered several times during the Lewis and Clark Expedition (1804–1806), though it was already well-known to European traders on the upper Missouri. Lewis, writing on May 5, 1805, in northeastern Montana, described the coyote as follows:<sup>[25]</sup>

the small wolf or burrowing dog of the prairies are the inhabitants almost invariably of the open plains; they usually associate in bands of ten or twelve sometimes more and burrow near some pass or place much frequented by game; not being able alone to take deer or goat they are rarely ever found alone but hunt in bands; they frequently watch and seize their prey near their burrows; in these burrows they raise their young and to them they also resort when pursued; when a person approaches them they frequently bark, their note being precisely that of the small dog. they are of an intermediate size between that of the fox and dog, very active fleet and delicately formed; the ears large erect and pointed the head long and pointed more like that of the fox; tale long; . . . the hair and fur also resembles the fox tho' is much coarser and inferior. they are of a pale redish brown colour. the eye of a deep sea green colour small and piercing. their tallons [claws] are reather longer than those of the ordinary wolf or that common to the atlantic states, none of which are to be found in this quarter, nor I believe above the river Plat.



Toltec pictograph of coyote.

The coyote was first scientifically described by Thomas Say in September 1819 on the site of Lewis and Clark's Council Bluffs, fifteen miles up the Missouri River from the mouth of the Platte during a government-

sponsored expedition with Major Stephen Long. He had the first edition of the Lewis and Clark journals in hand, which contained Biddle's edited version of Lewis's observations dated May 5, 1805.<sup>[26][27]</sup>

## Naming and etymology

The earliest written reference to the species comes from Francisco Hernández's *Plantas y Animales de la Nueva España* (1651), where it is described as a "Spanish fox" or "jackal". The first published usage of the word "coyote" (the root word of which is the Nahuatl *coyotl*) comes from Francisco Javier Clavijero's *Historia de México* in 1780.<sup>[28]</sup> The first time it was used in English occurred in William Bullock's *Six months' residence and travels in Mexico* (1824), where it is variously transcribed as *cayjotte* and *cocyotie*. The word's spelling was standardized as "coyote" by the 1880s.<sup>[25][29]</sup> Alternative English names for the coyote include "prairie wolf", "brush wolf", "cased wolf",<sup>[30][b]</sup> "little wolf"<sup>[7]</sup> and "American jackal".<sup>[31]</sup>

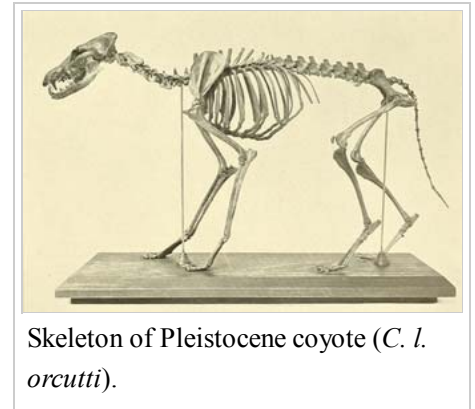
## Local and indigenous names

### Indigenous names for *Canis latrans*

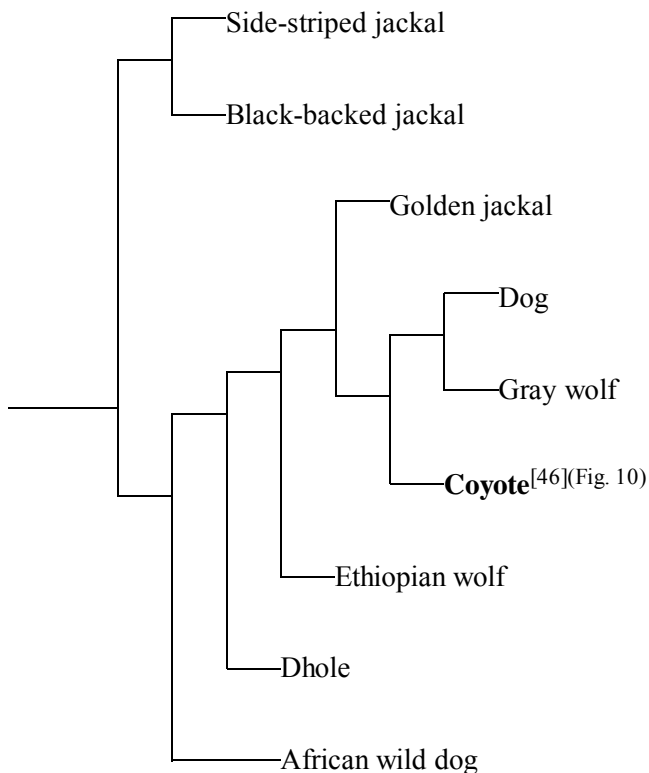
Linguistic group or area	Indigenous name
Arikara	<i>Stshirits pukatsh</i> <sup>[32]</sup>
Canadian French	<i>Coyote</i> <sup>[30]</sup>
Chinook	<i>Italipas</i> <sup>[32]</sup>
Chipewyan	<i>Nu-ní-yě=ɪs!é-lě</i> <sup>[33]</sup>
Cocopah	<i>Tɣpa</i> <sup>[34]</sup> <i>Xɣpa</i> <sup>[34]</sup>
Northern Cree	ᑭᑎᑭᑭᑭᑭ (Miscacâkanis) <sup>[35]</sup>
Plains Cree	ᑭᑎᑭᑭᑭᑭ (Mescacâkanis) <sup>[35]</sup>
Creek	ᖶ•hu•ce (archaic) <sup>[36]</sup> ᖶ•hv•la•nu•ce (modern) <sup>[36]</sup>
Dakota	<i>Mica</i> <sup>[32]</sup> <i>Micaksica</i> <sup>[32]</sup>
Flathead	<i>Sinchlep</i> <sup>[32]</sup>
Hidatsa	<i>Motsa</i> <sup>[32]</sup>
Hopi	<i>Iisawu</i> <sup>[37]</sup> <i>Isaw</i> <sup>[37]</sup>
Klamath	<i>Ko-ha-a</i> <sup>[32]</sup>
Mandan	<i>Scheke</i> <sup>[32]</sup>
Mayan	<i>Pek'i'cash</i> <sup>[38]</sup>
Nez Perce	<i>ɰiceyé•ye</i> <sup>[39]</sup>
Nahuatl	<i>Coyotl</i>
Navajo	<i>Ma'ii</i> <sup>[40]</sup>
Ogallala Sioux	<i>Mee-yah-slay'-cha-lah</i> <sup>[30]</sup>
Ojibwe	<i>Mes-ta-cha'-gan-es</i> <sup>[30]</sup>
Omaha	<i>Mikasi</i> <sup>[32]</sup>
Osage	<i>Šómɨhkasi</i> <sup>[41]</sup>
Pawnee	<i>Ckirihi</i> <sup>[42]</sup>
Piute	<i>Eja-ah</i> <sup>[32]</sup>
Spanish	<i>Coyote</i> <sup>[38]</sup> <i>Perro de monte</i> <sup>[38]</sup>
Yakima	<i>Telipa</i> <sup>[32]</sup>
Timbisha	<i>Isa(ppü)</i> <sup>[43]</sup> <i>Isapaippü</i> <sup>[43]</sup> <i>Itsappü</i> <sup>[43]</sup>
Wintu	<i>Ćarawa</i> <sup>[44]</sup> <i>Seder</i> <sup>[44]</sup>
Yankton Sioux	<i>Song-toke-cha</i> <sup>[30]</sup>

## Taxonomy and evolution

The earliest fossil carnivores that can be linked with some certainty to canids are the Eocene Miacids, which lived some 38 to 56 million years ago. The Miacids later diverged into caniforms and feliforms, with the former line leading to such genera as the coyote-sized *Mesocyon* of the Oligocene (38 to 24 million years ago), the fox-like *Leptocyon* and the wolf-like *Tomarctus* which inhabited North America some 10 million years ago.<sup>[45]</sup> The coyote represents a more primitive form of *Canis* than the gray wolf, as shown by its relatively small size and its comparatively narrow skull and jaws, which lack the grasping power necessary to hold the large prey wolves specialize in. This is further corroborated by the coyote's sagittal crest, which is low or totally flattened, thus indicating a weaker bite than the wolf's. The coyote is not a specialized carnivore as the wolf is, as shown by the larger chewing surfaces on the molars, reflecting the species' relative dependence on vegetable matter. In these respects, the coyote resembles the fox-like progenitors of the genus more so than the wolf.<sup>[2]</sup> Modern phylogenetics places the coyote between the gray wolf and golden jackal.<sup>[46]</sup>



Skeleton of Pleistocene coyote (*C. l. orcutti*).



The evolution of the coyote is remarkably well documented, and can be traced back in an unbroken line to the Hemphillian *Eucyon davisi*.<sup>[47]</sup> The coyote likely arose from a certain population of the Blancan species *C. lepophagus* which, although similar in weight to modern coyotes, had shorter limb bones, thus indicating a less cursorial lifestyle. Modern coyotes arose during the Middle Pleistocene, and showed much more variation than they do today.<sup>[2]</sup> Compared to their modern Holocene counterparts, Pleistocene coyotes (*C. l. orcutti*) were larger and more robust, likely in response to larger competitors and prey.<sup>[48]</sup> Pleistocene coyotes were likely more specialized carnivores than their descendants, as their teeth were more adapted to shearing meat, showing fewer grinding surfaces suited for processing vegetation.<sup>[49]</sup> Their reduction in size occurred within 1000 years of the Quaternary extinction event, when their large prey died out.<sup>[48]</sup> Furthermore, Pleistocene coyotes were unable to exploit the big game hunting niche left vacant after the extinction of the dire wolf, as it was rapidly filled by gray wolves, which likely actively killed off the large

coyotes, with natural selection favoring the modern gracile morph.<sup>[49]</sup>

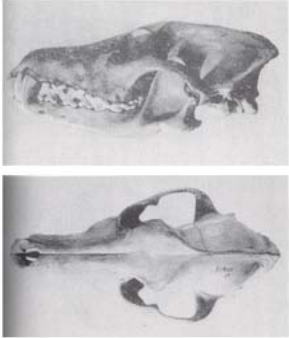
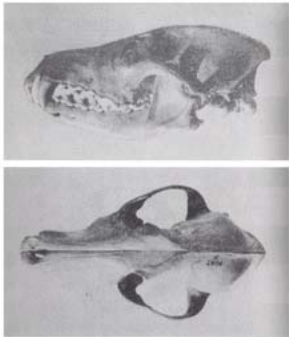
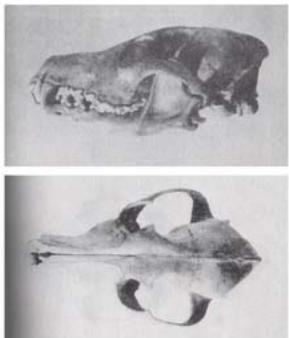
## Subspecies

As of 2005,<sup>[5]</sup> 19 subspecies are recognized. Geographic variation in coyotes is not great, though taken as a whole, the eastern subspecies (*thamnos* and *frustor*) are large, dark colored animals, with a gradual paling in color and reduction in size westward and northward (*texensis*, *latrans*, *lestes* and *incolatus*), a brightening of ochraceous tones towards the Pacific coast (*ochropus*, *umpquensis*), a reduction in size in the southwestern United States (*microdon*, *mearnsi*) and a general trend towards dark reddish colors and short muzzles in Mexican and Central American populations.<sup>[50]</sup>

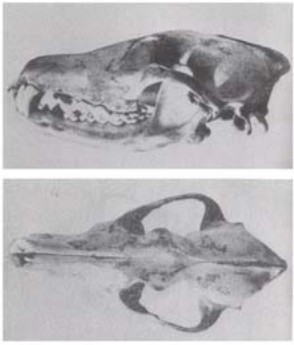
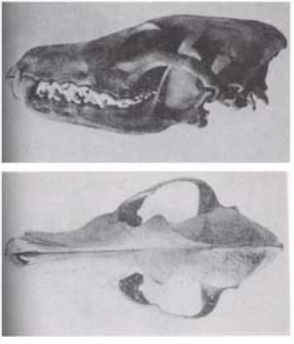
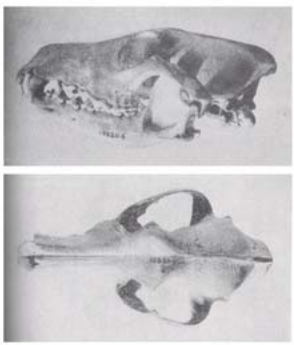
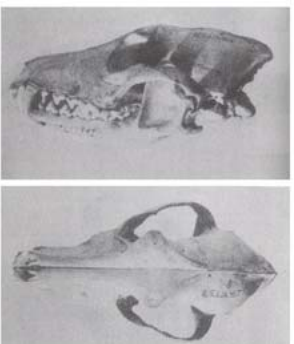


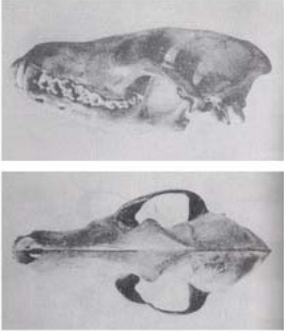
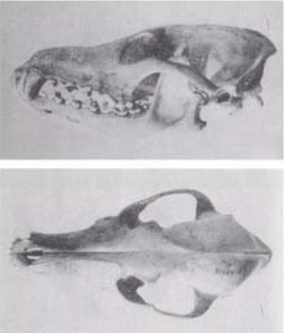
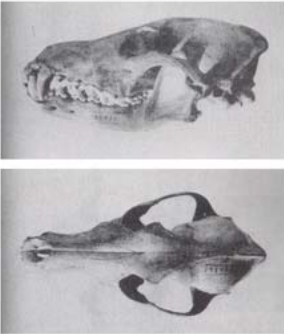
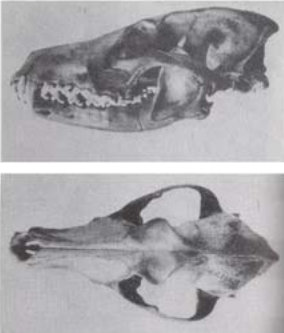
Range of coyote subspecies (as of 1978)

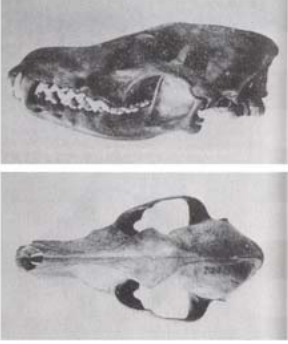
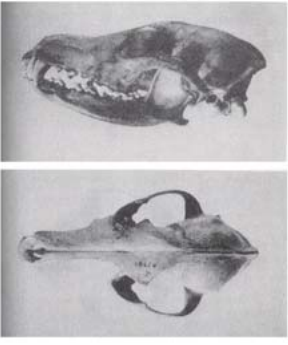
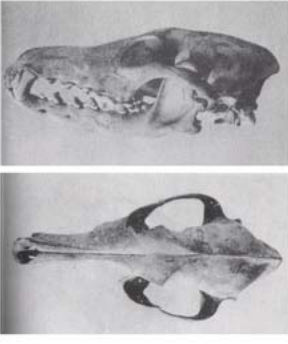
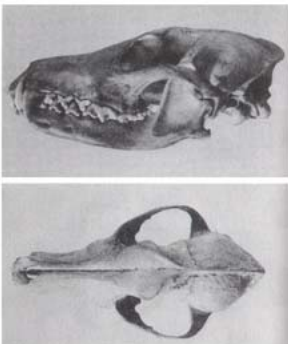


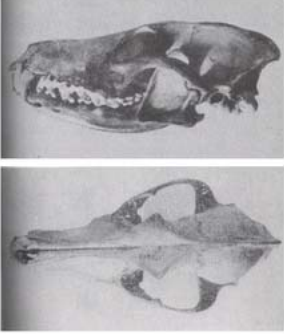
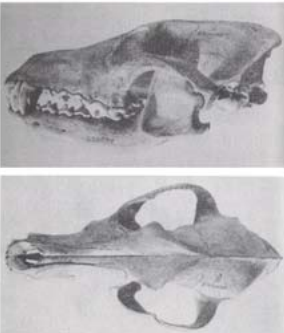
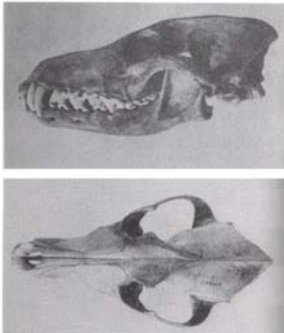
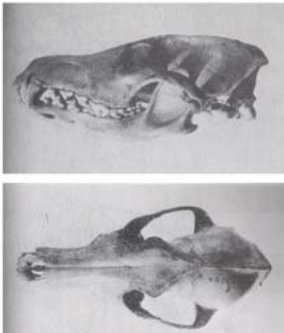
Subspecies	Trinomial authority	Description	Range	Synonyms
<p><b>Plains coyote</b>  <i>C. l. latrans</i>  Nominate subspecies</p> 	Say, 1823	The largest subspecies, with rather pale fur and bearing large molars and carnassials. <sup>[51]</sup>	Great Plains from Alberta, Manitoba, and Saskatchewan south to New Mexico and the Texas Panhandle	<i>nebracensis</i> (Merriam, 1898) <i>pallidus</i> (Merriam, 1897)
<p><b>Mexican coyote</b>  <i>C. l. cagottis</i></p> 	C. E. H. Smith, 1839	Similar to <i>peninsulae</i> , but larger and redder in color, with shorter ears, larger teeth and a broader muzzle. <sup>[51]</sup>	States of Oaxaca, San Luis Potosi, Puebla, and Veracruz in Mexico	
<p><b>San Pedro Martir coyote</b>  <i>C. l. clepticus</i></p> 	Elliot, 1903	A small subspecies with reddish summer fur and a short, broad skull. <sup>[52]</sup>	Northern Baja California and southwestern California	
<p><b>Salvador coyote</b>  <i>C. l. dickeyi</i></p>	Nelson, 1932	A large subspecies, equalling <i>lestes</i> in size, but has smaller teeth and darker fur. <sup>[53]</sup>	Originally only known from Cerro Mogote, two miles west of the Goascorán River in La Unión, El Salvador. <sup>[53]</sup> In January 2013, it expanded its range southward to southern Panama. <sup>[4]</sup>	



				
<p><b>Southeastern coyote</b> <i>C. l. frustor</i></p> 	Woodhouse, 1851	Similar to <i>peninsulae</i> , but larger and paler, with shorter ears and a longer muzzle. <sup>[51]</sup>	Southeastern and extreme eastern Kansas, Oklahoma, Texas, Missouri, and Arkansas	
<p><b>Belize coyote</b> <i>C. l. goldmani</i></p> 	Merriam, 1904	Largest of the Mexican coyotes, approaching <i>latrans</i> in size, but has a shorter muzzle. <sup>[54]</sup>	Known only from San Vicente, Chiapas, Mexico, near the Guatemalan border, though it could be the coyote of western Guatemala.	
<p><b>Honduras coyote</b> <i>C. l. hondurensis</i></p> 	Goldman, 1936	A small, rufous-colored subspecies with coarse, thin fur and a broad skull. <sup>[55]</sup>	Known only from the open country northeast of Archaga, north of Tegucigalpa	
<p><b>Durango coyote</b> <i>C. l. impavidus</i></p>	J. A. Allen, 1903	Similar to <i>cagottis</i> in color, but much larger. <sup>[52]</sup>	Southern Sonora, extreme southwestern Chihuahua, western	

			Durango, western Zacatecas, and Sinaloa	
<p><b>Northern coyote</b> <i>C. l. incolatus</i></p> 	Hall, 1934	A medium-sized subspecies, with cinnamon-colored fur and a more concave skull than <i>latrans</i> . <sup>[56]</sup>	Yukon, Northwest Territories, northern British Columbia, and northern Alberta, and Alaska	
<p><b>Tiburón Island coyote</b> <i>C. l. jamesi</i></p> 	Townsend, 1912	Much paler than <i>mearnsi</i> , with heavier teeth, a large skull, and long ears. <sup>[57]</sup>	Tiburón Island	
<p><b>Mountain coyote</b> <i>C. l. lestes</i></p> 	Merriam, 1897	Similar in size and color to <i>latrans</i> , with a large tail and ears. <sup>[51]</sup>	British Columbia and southeastern Alberta south to Utah and Nevada	
<p><b>Mearns' coyote</b> <i>C. l. mearnsi</i></p>	Merriam, 1897	A small subspecies with medium-sized ears, a small skull and small	Southwestern Colorado and southern Utah south to northern Sonora and	<i>estor</i> (Merriam, 1897)

		<p>teeth. The fur is richly and brightly colored. The fulvous tints are exceedingly bright, and cover the hind and forefeet.<sup>[51]</sup></p>	Chihuahua	
<p><b>Lower Rio Grande coyote</b> <i>C. l. microdon</i></p> 	Merriam, 1897	<p>A small subspecies, with small teeth and rather dark fur. The upper surface of the hind foot is whitish, while the belly is sprinkled with black-tipped hairs.<sup>[51]</sup></p>	Southern Texas and northern Tamaulipas	
<p><b>California Valley coyote</b> <i>C. l. ochropus</i></p> 	Eschscholtz, 1829	<p>Similar to <i>latrans</i> and <i>lestes</i>, but smaller, darker, more brightly colored, has larger ears and smaller skull and teeth.<sup>[51]</sup></p>	California west of the Sierra Nevada	
<p><b>Peninsula coyote</b> <i>C. l. peninsulae</i></p> 	Merriam, 1897	<p>Similar to <i>ochropus</i> in size and features, but has darker, redder fur. The underside of the tail is blacker than that of <i>ochropus</i>, and the belly has more black-tipped hairs.<sup>[51]</sup></p>	Baja California	

<p><b>Texas Plains coyote</b> <i>C. l. texensis</i></p> 	Bailey, 1905	Smaller than <i>latrans</i> , with brighter, more fulvous fur closely approaching the richness found in <i>ochropus</i> , though <i>texensis</i> lacks that subspecies' large ears. <sup>[58]</sup>	most of Texas, eastern New Mexico, and northeastern Mexico	
<p><b>Northeastern coyote</b> <i>C. l. thamnus</i></p> 	Jackson, 1949	About the same size as <i>latrans</i> , or larger, but darker in color, and has a broader skull. <sup>[59]</sup>	From north-central Saskatchewan east to southern Ontario, south to northern Indiana and west to Missouri	
<p><b>Northwest Coast coyote</b> <i>C. l. umpquensis</i></p> 	Jackson, 1949	A small subspecies, with dark, rufous-tinged fur, a comparatively small skull and weak dentition. <sup>[59]</sup>	Coast of Washington and Oregon	
<p><b>Colima coyote</b> <i>C. l. vigilis</i></p> 	Merriam, 1897	Similar to <i>peninsulae</i> , but darker and more extensively colored, with more black on the forearm, and no black on the underside of the tail (excepting the tip). <sup>[51]</sup>	Pacific coast of Mexico from Jalisco south to Guerrero	

## Hybridization

Coyotes have occasionally mated with dogs, sometimes producing crosses capable of work.<sup>[60]</sup> Such matings are rare in the wild, as the mating cycles of dogs and coyotes do not coincide, and coyotes are usually antagonistic towards dogs, with even captive specimens having shown reluctance to mate with them. Hybridization usually only occurs when coyotes are expanding into areas where conspecifics are few, and dogs are the only alternatives. Even then, pup survival rates are lower than normal, as dogs do not form pair bonds with coyotes, thus making the rearing of pups more difficult.<sup>[61]</sup> In captivity, F<sub>1</sub> hybrids tend to be more mischievous and less manageable as pups than dogs, and are less trustworthy on maturity than wolf-dog hybrids.<sup>[60]</sup> Hybrids vary in appearance, but generally retain the coyote's adult sable coat color, dark neonatal coat color, bushy tail with an active supracaudal gland, and white facial mask. F<sub>1</sub> hybrids tend to be intermediate in form between dogs and coyotes, while F<sub>2</sub> hybrids are more varied. Both F<sub>1</sub> and F<sub>2</sub> hybrids resemble their coyote parents in terms of shyness and intrasexual aggression.<sup>[62]</sup> Hybrid play behavior includes the coyote "hip-slam".<sup>[63]</sup> Hybrids of both sexes are fertile, and can be successfully bred through four generations.<sup>[60]</sup> Melanistic coyotes owe their black pelts to a mutation that first arose in domestic dogs.<sup>[64]</sup> A population of non-albino white coyotes in Newfoundland owe their coloration to a MC1R mutation inherited from golden retrievers.<sup>[65]</sup>

Coyotes have hybridized with wolves to varying degrees, particularly in the Eastern United States and Canada. The so-called "eastern coyote" of northeastern North America has been confirmed to be of mixed wolf-coyote parentage, and probably originated in the aftermath of the extermination of wolves in the northeast, thus allowing coyotes to colonize former wolf ranges and mix with remnant wolf populations. This hybrid is smaller than the wolf, and holds smaller territories, but is in turn larger and holds more extensive home ranges than the typical western coyote. As of 2010, the eastern coyote's genetic makeup is fairly uniform, with minimal influence from eastern wolves or western coyotes.<sup>[66]</sup> Adult eastern coyotes are larger than western coyotes, weighing an average of 30–40 lbs, with female eastern coyotes weighing 21% more than male western coyotes.<sup>[66][67]</sup> Eastern coyotes also weigh more at birth; while newborn western coyotes weigh 250–300 grams, eastern coyotes weigh 349–360 grams. By the age of 35 days, eastern coyote pups average 1590 grams, 200 grams more than western coyotes of similar age. By this time, physical differences become more apparent, with eastern coyote pups having longer legs than their western counterparts. Differences in dental development also occur, with tooth eruption being later, and in a different order in the eastern coyote.<sup>[68]</sup> Aside from its size, the eastern coyote is physically not unlike the western coyote; both have erect ears, a straight and bushy tail, a conspicuous supracaudal gland and a narrow chest. There are four color phases, ranging from dark brown to blond or reddish blond, though the most common phase is gray-brown, with reddish legs, ears and flanks.<sup>[69]</sup> There are no significant differences between eastern and western coyotes in expressing aggression and fighting, though eastern coyotes tend to fight less, and are more playful. Unlike western coyote pups, in which fighting precedes play behavior, fighting among eastern coyote pups occurs after the onset of play.<sup>[68]</sup> Eastern coyotes tend to reach sexual maturity when they reach two years of age, much later than in western coyotes.<sup>[66]</sup> In 2011, an analysis of 48,000 SNP chips in the genomes of various wolf and coyote populations revealed that the eastern wolf (native to Algonquin Provincial Park) and the red wolf (native to North Carolina), both previously labeled as species distinct from the gray wolf, are in fact products of varying degrees of wolf-coyote hybridization. The wolf-coyote admixture resulting in the development of the eastern wolf may have occurred on the order of 600–900 years ago between gray wolves and a now extinct pre-Columbian coyote population. The eastern wolf has since backcrossed extensively with parent gray wolf populations. The red wolf may have originated later, approximately 287–430 years ago, when much of the southeastern U.S. was being converted to agriculture and predators



Coywolf hybrid conceived in captivity between a male gray wolf and a female coyote.



were targeted for extermination. During this period, declining local wolf populations would have been forced to mate with coyotes, with the resulting hybrids backcrossing to coyotes as the wolves disappeared, to the extent that ~75–80% of the modern red wolf's genome is of coyote derivation.<sup>[70]</sup>

## Behavior

### Social and reproductive behaviors

Like the golden jackal, the coyote is gregarious, but not as dependent on conspecifics as more social canid species like wolves are. This is likely linked to the fact that the coyote is not a specialized hunter of large prey as the latter species is.<sup>[71]</sup> The basic social unit of a coyote pack is a nuclear family centered around a reproductive female.

However, unrelated coyotes may join forces for companionship, or to bring down prey too large to attack singly. Such "non-family" packs are only temporary, and may consist of bachelor males,

non-reproductive females and sub-adult young. Families are formed in midwinter, when females enter estrus.<sup>[7]</sup> Pair bonding can occur 2–3 months before actual copulation takes place. A female entering estrus attracts males by scent marking and howling with increasing frequency.<sup>[31]</sup> A single female in heat can attract up to seven reproductive males, which can follow her for as much as a month.

Although there may be some squabbling among the males, once the female has selected a mate and copulates, the rejected males do not

intervene, and move on once they detect other estrous females.<sup>[7]</sup> Unlike the wolf, which has been known to practice both monogamous and bigamous matings,<sup>[72]</sup> the coyote is strictly monogamous, even in areas with high coyote densities and abundant food.<sup>[73]</sup> Females that fail to mate sometimes assist their sisters or mothers in raising their pups, or will join their siblings until the next time they can mate. The newly mated pair then establish a territory and either construct their own den or clean out abandoned badger, marmot or skunk earths. During the pregnancy, the male frequently hunts alone and brings back food for the female. The female may line the den with dried grass or with fur pulled from her belly.<sup>[7]</sup> The gestation period lasts 63 days, with an average litter size of six, though the number fluctuates depending on coyote population density and the abundance of food.<sup>[31]</sup>

Coyote pups are born in dens, hollow trees, or under ledges, and weigh 200-50 grams at birth. They are altricial, and are completely dependent on milk for their first 10 days. The incisors erupt at about 12 days, the canines at 16, and the second premolars at 21. Their eyes open after 10 days, by which point the pups become increasingly more mobile, walking by 20 days, and running at the age of six weeks. The parents begin supplementing the pup's diet with regurgitated solid food after 12–15 days. By the age of 4–6 weeks, when their milk teeth are fully functional, the pups are given small food items like mice, rabbits or pieces of ungulate carcasses, with lactation steadily decreasing after two months.<sup>[7]</sup> Unlike wolf pups, coyote pups begin seriously fighting prior to engaging in play behavior. By 3 weeks of age, coyote pups bite each other with less inhibition than wolf pups. By the age of 4–5 weeks, pups have established dominance hierarchies, and are by then more likely to play rather than fight.<sup>[74]</sup> The male plays an active role in feeding, grooming and guarding the pups, but will abandon them if the female goes missing before the pups are completely weaned. The den is abandoned by June–July, and the pups follow their parents in patrolling their territory and hunting. Pups may leave their families in August, though can remain for much longer. The pups attain adult dimensions at eight months, and gain adult weight a month later.<sup>[7]</sup>

### Territorial and sheltering behaviors



Mearns' coyote (*C. l. mearnsi*) pups playing.

Individual feeding territories vary in size from 0.38 to 62 km<sup>2</sup> (0.15 to 23.94 sq mi), with the general concentration of coyotes in a given area depending on food abundance, adequate denning sites, and competition with conspecifics and other predators. The coyote generally does not defend its territory outside of the denning season,<sup>[7]</sup> and is much less aggressive towards intruders than the wolf is, typically chasing and sparring with them, but rarely killing them.<sup>[75]</sup> Conflicts between coyotes can arise during times of food shortage.<sup>[7]</sup>

Like wolves, coyotes use a den (usually the deserted holes of other species) when gestating and rearing young, though they may occasionally give birth under sagebrushes in the open. Coyote dens can be located in canyons, washouts, coulees, banks, rock bluffs, or level ground. Some dens have been found under abandoned homestead shacks, grain bins, drainage pipes, railroad tracks, hollow logs, thickets and thistles. The den is continuously dug and cleaned out by the female until the pups are born. Should the den be disturbed or infested with fleas, the pups are moved into another den. A coyote den can have several entrances and passages branching out from the main chamber.<sup>[76]</sup> A single den can be used year after year.<sup>[31]</sup>

## Hunting and feeding behaviors

When hunting large prey, the coyote often works in pairs or in small groups.<sup>[16]</sup> Success in killing large ungulates depends on factors such as snow depth and crust density. Younger animals usually avoid participating in such hunts, with the breeding pair typically doing most of the work.<sup>[31]</sup> Unlike the wolf, which attacks large prey from the rear, the coyote approaches from the front, lacerating its prey's head and throat. Like other canids, the coyote caches excess food.<sup>[77]</sup> Coyotes catch mouse-like rodents by pouncing, whereas ground squirrels are chased. Although coyotes can live in large groups, small prey is typically caught singly.<sup>[31]</sup> Coyotes have been observed to kill porcupines in pairs, using their paws to flip the rodents on their backs, then attacking the soft underbelly. Only old and experienced coyotes can successfully prey on porcupines, with many predation attempts by young coyotes resulting in them being injured by their prey's quills.<sup>[78]</sup> Coyotes sometimes urinate on their food, possibly to claim ownership over it.<sup>[79]</sup>

## Ecology

### Habitat

Prior to the near extermination of wolves and cougars, the coyote was most numerous in grasslands inhabited by bison, antelope, elk and other deer, doing particularly well in short grass areas with prairie dogs, though it was just as much at home in semiarid areas with sagebrush and jackrabbits or in deserts inhabited by cactus, kangaroo rats and rattlesnakes. As long as it was not in direct competition with the wolf, the coyote ranged from the Sonoran Desert to the alpine regions of adjoining mountains or the plains and mountainous areas of Alberta. With the extermination of the wolf, the coyote's range expanded to encompass broken forests from the tropics of Guatemala and the northern slope of Alaska.<sup>[7]</sup>

### Diet

The coyote is highly versatile in its choice of food, but is primarily carnivorous, with 90% of its diet consisting of animal matter. Prey species include bison, deer, sheep, rabbits, rodents, birds, amphibians (except toads), lizards, snakes, fish, crustaceans, and insects. Coyotes may be picky over the prey they target, as animals such as shrews, moles and brown rats do not occur in their diet in proportion to their numbers.<sup>[7]</sup> More unusual prey include fishers,<sup>[80]</sup> young black bears,<sup>[81]</sup> harp seals<sup>[82]</sup> and rattlesnakes. Although coyotes prefer fresh meat, they will scavenge when the opportunity presents itself. It has been estimated that, excluding the insects, fruit and grass eaten, the coyote requires 600 g of food daily, or 250 kg annually.<sup>[7]</sup> The coyote readily cannibalizes the carcasses of conspecifics, with coyote fat having been successfully used by



coyote hunters as a lure or poisoned bait.<sup>[18]</sup> The coyote's winter diet consists mainly of large ungulate carcasses, with very little vegetable matter. Rodent prey increases in importance during the spring, summer, and fall.<sup>[16]</sup>

The coyote feeds on a variety of different fruits, including blackberries, blueberries, peaches, pears, apples, prickly pears, chapotes, persimmons, and peanuts. Other vegetable foods include watermelon, cantaloupe and carrots. During the winter and early spring, the coyote eats large quantities of grass, such as green wheat blades. It sometimes eats unusual items like cotton cake, soybean meal, domestic animal droppings, and cultivated grain such as corn, wheat, sorghum, and beans.<sup>[7]</sup>

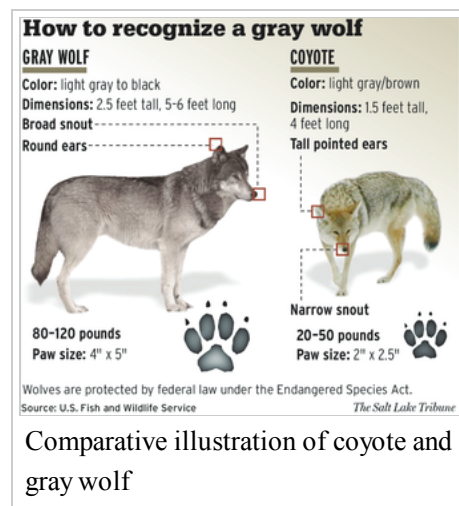
## Enemies and competitors

In areas where the ranges of coyotes and gray wolves overlap, interference competition and predation by wolves has been hypothesized to limit local coyote densities. Coyote ranges expanded during the 19th and 20th centuries following the extirpation of wolves, while coyotes were driven to extinction on Isle Royale after wolves colonized the island in the 1940s. One study conducted in Yellowstone National Park, where both species coexist, concluded that the coyote population in the Lamar River Valley declined by 39% following the reintroduction of wolves in the 1990s, while coyote populations in wolf inhabited areas of the Grand Teton National Park are 33% lower than in areas where they are absent.<sup>[10]</sup> Wolves have been observed to not tolerate coyotes in their vicinity, though coyotes have been known to trail wolves in order to feed on their kills.<sup>[83]</sup>

Coyotes rarely kill healthy adult red foxes, and have been observed to feed or den alongside them, though they often kill foxes caught in traps. Coyotes may kill fox kits, but this is not a major source of mortality.<sup>[84]</sup> In southern California, coyotes frequently kill gray foxes, and these smaller canids tend to avoid areas with high coyote densities.<sup>[85]</sup>

Coyotes may compete with cougars in some areas. In eastern Sierra Nevada, coyotes compete with cougars over mule deer. Cougars usually outcompete coyotes, and may kill them occasionally, thus reducing coyote predation pressure on smaller carnivores like foxes and bobcats.<sup>[9]</sup>

In some areas, coyotes share their ranges with bobcats. It is rare for these two similarly sized species to physically confront one another, though bobcat populations tend to diminish in areas with high coyote densities.<sup>[86]</sup> However, several studies have demonstrated interference competition between coyotes and bobcats, and in all cases coyotes dominated the interaction.<sup>[87]</sup> Multiple researchers<sup>[88][89][90][91][92]</sup> all reported instances of coyotes killing bobcats, whereas bobcats killing coyotes is more rare.<sup>[87]</sup> Coyotes attack bobcats using a bite-and-shake method similar to that used on medium-sized prey. Coyotes (both single individuals and groups) have been known to occasionally kill bobcats – in most cases, the bobcats were relatively small specimens, such as adult females and juveniles.<sup>[91]</sup> However, coyote attacks (by an unknown number of coyotes) on adult male bobcats have occurred. In California, coyote and bobcat populations are not negatively correlated across different habitat types, but predation by coyotes is an important source of mortality in bobcats.<sup>[85]</sup> Biologist Stanley Paul Young noted that in his entire trapping career, he had never successfully saved a captured bobcat from being killed by coyotes, and wrote of two incidences wherein coyotes chased bobcats up trees.<sup>[83]</sup> Coyotes have been documented to directly kill Canadian lynx on



Mountain coyotes (*C. l. lestes*) cornering a juvenile cougar

occasion,<sup>[93][94]</sup> and compete with them for prey, especially snowshoe hares.<sup>[93]</sup> In some areas, including central Alberta, lynx are more abundant where coyotes are few, thus interactions with coyotes appears to influence lynx populations more than the availability of snowshoe hares.<sup>[95]</sup>

Coyotes may occasionally form commensal relationships with badgers, assisting each other in digging up rodent prey. The relationship between the two species may occasionally border on apparent friendship, as some coyotes have been observed to lay their heads on their badger companions or lick their faces without protest. The amicable interactions between coyotes and badgers were known to pre-Columbian civilizations, as shown on a Mexican jar dated to 1250–1300 AD depicting the relationship between the two.<sup>[83]</sup>

## Communication

### Body language

Being both a gregarious and solitary animal, the variability of the coyote's visual and vocal repertoire is intermediate between that of the solitary foxes and the highly social wolf.<sup>[71]</sup> The aggressive behavior of the coyote bears more similarities to that of foxes than it does that of wolves and dogs. An aggressive coyote arches its back and lowers its tail.<sup>[96]</sup> Unlike dogs, which solicit playful behavior by performing a "play-bow" followed by a "play-leap", play in coyotes consists of a bow, followed by side-to-side head flexions and a series of "spins" and "dives". Although coyotes will sometimes bite their playmates' scruff as dogs do, they typically approach low, and make upward directed bites.<sup>[97]</sup> Pups will fight each other regardless of sex, while among adults aggression is typically reserved for members of the same sex. Combatants approach each other waving their tails and snarling with their jaws open, though fights are typically silent. Males tend to fight in a vertical stance, while females fight on all four paws. Fights among females tend to be more serious than ones among males, as females seize their opponents' forelegs, throat and shoulders.<sup>[96]</sup>

### Vocalizations

The coyote has been described as "the most vocal of North American wild mammals...", whose vocal proclivity lead to its being given the binomial name *Canis latrans*, meaning "barking dog". At least 11 different vocalizations are known in adult coyotes. These sounds are divided into three categories: 1) Agonistic and alarm, 2) Greeting, and 3) Contact. Vocalizations of the first category include woofs, growls, huffs, barks, bark howls, yelps and high frequency whines. Woofs are used as low intensity threats or alarms, and are usually heard near den sites, prompting the pups to immediately retreat into their burrows. Growls are used as threats in short distances, but have also been heard among pups playing and copulating males. Huffs are high intensity threat vocalizations produced via rapid expiration of air. Barks can be classed as both long distance threat vocalizations and as alarm calls. Bark howls may serve similar functions. Yelps are emitted as a sign of submission, while high frequency whines are produced by dominant animals acknowledging the submission of subordinates. Greeting vocalizations include low frequency whines, *wow-oo-wows* and group yip howls. Low frequency whines are emitted by submissive animals, and are usually accompanied by tail wagging and muzzle nibbling. The sound known as *wow-oo-wow* has been described as a "greeting song". The group yip howl is emitted when two or more pack members reunite, and may be the final act of a complex greeting ceremony. Contact calls include lone howls and group howls, as well as the previously mention group yip howls. The lone howl is the most iconic sound of the coyote, and may serve the purpose of announcing the presence of a lone individual separated from its pack. Group howls are used as both substitute group yip howls and as responses to either lone howls, group howls or group yip howls.<sup>[8]</sup>

## Range

The coyote's pre-Columbian range was limited to the south-west and plains regions of the U.S. and Canada, and northern and central Mexico. By the 19th century, the species expanded north and west, expanding

further after 1900, coinciding with land conversion and the extirpation of wolves. By this time, its range encompassed all of the U.S. and Mexico, southward into Central America, and northward into most of Canada and Alaska. This expansion is ongoing, and the species now occupies the majority of areas between 8°N (Panama) and 70°N (northern Alaska).<sup>[1]</sup>

## In Mexico and Central America

Although it was once widely believed that coyotes are recent immigrants to southern Mexico and Central America, aided in their expansion by deforestation, Pleistocene-Early Holocene records, as well as records from the Pre-Columbian period and early European colonization show that the animal was present in the area long before modern times. Nevertheless, range expansion did occur south of Costa Rica during the late 1970s and northern Panama in the early 1980s, following the expansion of cattle grazing lands into tropical rainforests. It has been predicted that the coyote should appear in northern Belize in the near future, as the habitat there is favorable to the species.<sup>[98]</sup> Concerns have been raised of a possible expansion into South America through the Panamanian Isthmus, should the Darién Gap ever be closed by the Pan-American Highway.<sup>[99]</sup> This fear was partially confirmed in January 2013, when the species was recorded in eastern Panama's Chepo District, beyond the Panama Canal.<sup>[4]</sup>

## Diseases and parasites

Among large North American carnivores, the coyote probably carries the largest number of diseases and parasites, likely due to its wide range and varied diet.<sup>[100]</sup> Viral diseases known to infect coyotes include rabies, canine distemper, infectious canine hepatitis, four strains of equine encephalitis, and oral papillomatosis. By the late 1970s, serious rabies outbreaks in coyotes had ceased to be a problem for over 60 years, though sporadic cases every 1–5 years did occur. Distemper causes the deaths of many pups in the wild, though some specimens can survive infection. Tularemia, a bacterial disease, infects coyotes through their rodent and lagomorph prey, and can be deadly for pups.<sup>[101]</sup>

Coyotes can be infected by both demodectic and sarcoptic mange, the latter being the most common. Mite infestations are rare and incidental in coyotes, while tick infestations are more common, with seasonal peaks depending on locality (May–August in the Northwest, March–November in Arkansas). Coyotes are only rarely infested with lice, while fleas infest coyotes from puphood, though they may be more a source of irritation than serious illness. *Pulex simulans* is the most common species to infest coyotes, while *Ctenocephalides canis* tends to occur only in areas where coyotes and dogs (its primary host) inhabit the same area. Although coyotes are rarely host to flukes, they can nevertheless have serious effects on coyotes, particularly *Nanophyetus salmincola*, which can infect them with salmon poisoning disease, a fatal disease with a 90% mortality rate. Tapeworms have been recorded to infest 60–95% of all coyotes examined. The most common species to infest coyotes is *Taenia pisiformis* and *Taenia crassiceps*, which uses cottontail rabbits as intermediate hosts. The largest species known in coyotes is *T. hydatigena*, which enters coyotes through infected ungulates, and can grow to lengths of 800–4000 mm. Though once largely limited to wolves, *Echinococcus granulosus* has expanded to coyotes since the latter began colonizing former wolf ranges. The most frequent ascaroid roundworm in coyotes is *Toxascaris leonina*, which dwells in the coyote's short intestine and has no ill effects, save for causing the host to eat more frequently. Hookworms of the genus *Ancylostoma* infest coyotes throughout their range, being particularly prevalent in humid areas. In areas of high moisture, such as coastal Texas, coyotes can carry up to 250 hookworms each. The blood-drinking *A. caninum* is particularly dangerous, as it damages the coyote through blood-loss and lung congestion. A 10-day-old pup can die from being host to as few as 25 *A. caninum*.<sup>[101]</sup>



California Valley coyote (*C. l. ochropus*) suffering from sarcoptic mange.

## Relationships with humans

### In folklore and mythology

The coyote features prominently as a trickster figure in the folktales of America's indigenous peoples, alternately assuming the form of an actual coyote or a man. As with other trickster figures, the coyote acts as a picaresque hero which rebels against social convention through deception and humor.<sup>[11]</sup> The coyote was likely given its trickster role in light of the actual animal's intelligence and adaptability; pre-Columbian American people observed its behavior, and their folkloric representations reflected its attributes.<sup>[102]</sup> It is variously credited for having brought fire to humanity, releasing the bison into the world, and of having slain monsters by petrifying them. The Maidu creation myth has the coyote introducing work, suffering and death to the world. Zuni folklore has the coyote bringing winter into the world by stealing light from the kachinas. Some tribes, such as the Chinook, Maidu, Paiute, Pawnee, Tohono O'odham, and Ute portray the coyote as the companion of the creator. In the Paiute creation myth, the coyote was created by the wolf as a companion, and the two created land by piling dirt on the water-covered world. A Tohono O'odham flood myth has the coyote helping Montezuma survive a global deluge that destroys humanity. After the Great Mystery creates humanity, the coyote and Montezuma teach people how to live. The Crow creation myth portrays Old Man Coyote as the creator. In Navajo mythology, the coyote was present in the First World with First Man and First Woman, though a different version has it being created in the Fourth World. The Navajo coyote brings death into the world, explaining that without death, there would be too many people, and thus no room to plant corn.<sup>[103]</sup>



Spirit shield fashioned from coyote skull and crow feathers.

Prior to the Spanish conquest of the Aztec Empire, the coyote played a significant role in Mesoamerican cosmology. The coyote symbolized military might in pre-Aztec Teotihuacan, with warriors dressing up in coyote costumes to call upon its predatory power. The species continued to be linked to Central Mexican warrior cults in the centuries leading up to Aztec rule.<sup>[12]</sup> In Aztec mythology, Huehucóyotl (meaning "old coyote"), the god of dance, music and carnality, is depicted in several codices as a man with a coyote's head.<sup>[104]</sup> He is sometimes depicted as a womanizer, responsible for bringing war into the world by seducing Xochiquetzal, the goddess of love.<sup>[105]</sup> Epigrapher David H. Kelley argued that the god Quetzalcoatl owed its origins to pre-Aztec Uto-Aztecan mythological depictions of the coyote, which is portrayed as mankind's "Elder Brother", a creator, seducer, trickster and culture hero linked to the morning star.<sup>[13]</sup>

### Attacks on humans

Coyote attacks on humans are uncommon and rarely cause serious injuries, due to the relatively small size of the coyote, but have been increasingly frequent, especially in the state of California. In the 30 years leading up to March 2006, at least 160 attacks occurred in the United States, mostly in the Los Angeles County area.<sup>[106]</sup> Data from USDA Wildlife Services, the California Department of Fish and Game, and other sources show that while 41 attacks occurred during the period of 1988–1997, 48 attacks were verified from 1998 through 2003. The majority of these incidents occurred in Southern California near the suburban-wildland interface.<sup>[107]</sup>

In the absence of the harassment of coyotes practiced by rural people, urban coyotes are losing their fear of humans, which is further worsened by people intentionally or unintentionally feeding coyotes. In such situations, some coyotes have begun to act aggressively toward humans, chasing joggers and bicyclists,



confronting people walking their dogs, and stalking small children.<sup>[107]</sup> Non rabid coyotes in these areas will sometimes target small children, mostly under the age of 10, though some adults have been bitten.

Although media reports of such attacks generally identify the animals in question as simply "coyotes," research into the genetics of the eastern coyote indicates those involved in attacks in northeast North America, including Pennsylvania, New York, New England, and eastern Canada, may have actually been coywolves, hybrids of *Canis latrans* and *Canis lupus*, not fully coyotes.<sup>[108]</sup>

## Livestock and pet predation

Coyotes are presently the most abundant livestock predators in western North America, causing the majority of sheep, goat and cattle losses.<sup>[109]</sup> For example, according to the National Agricultural Statistics Service, coyotes were responsible for 60.5% of the 224,000 sheep deaths attributed to predation in 2004.<sup>[110]</sup> The total number of sheep deaths in 2004 comprised 2.22% of the total sheep and lamb population in the United States.<sup>[111]</sup> According to the National Agricultural Statistics Service USDA report, "All sheep and lamb inventory in the United States on July 1, 2005, totaled 7.80 million head, 2% above July 1, 2004. Breeding sheep inventory at 4.66 million head on July 1, 2005 was 2% above July 1, 2004."<sup>[112]</sup> Because coyote populations are typically many times greater and more widely distributed than those of wolves, coyotes cause more overall predation losses. However, an Idaho census taken in 2005 showed that individual coyotes were one-twentieth as likely to attack livestock than individual wolves.<sup>[113]</sup>

Livestock guardian dogs are commonly used to aggressively repel predators and have worked well in both fenced pasture and range operations. A 1986 survey of sheep producers in the USA found that 82% reported the use of dogs represented an economic asset.<sup>[114][115]</sup>

Coyotes will typically bite the throat just behind the jaw and below the ear when attacking adult sheep or goats, with death commonly resulting from suffocation. Blood loss is usually a secondary cause of death. Calves and heavily fleeced sheep are killed by attacking the flanks or hindquarters, causing shock and blood loss. When attacking smaller prey, such as young lambs, the kill is made by biting the skull and spinal regions, causing massive tissue and bone damage. Small or young prey may be completely carried off, leaving only blood as evidence of a kill. Coyotes will usually leave the hide and most of the skeleton of larger animals relatively intact, unless food is scarce, in which case they may leave only the largest bones. Scattered bits of wool, skin and other parts are characteristic where coyotes feed extensively on larger carcasses.<sup>[109]</sup>

Coyote predation can usually be distinguished from dog or coydog predation by the fact that coyotes partially consume their victims. Tracks are also an important factor in distinguishing coyote from dog predation. Coyote tracks tend to be more oval-shaped and compact than those of domestic dogs, and their claw marks are less prominent and the tracks tend to follow a straight line more closely than those of dogs. With the exception of sighthounds, most dogs of similar weight to coyotes have a slightly shorter stride.<sup>[109]</sup> Coyote kills can be distinguished from wolf kills by the fact that there is less damage to the underlying tissues. Also, coyote scats tend to be smaller than wolf scats.<sup>[116]</sup>

The U.S. government routinely shoots, poisons, traps and kills about 90,000 coyotes each year to protect livestock.<sup>[117]</sup>



A sign discouraging people from feeding coyotes, which can lead to them habituating themselves to human presence, thus increasing the likelihood of attack



Coyote confronting a dog



Coyote with a typical throat hold on domestic sheep

Coyotes are often attracted to dog food and animals that are small enough to appear as prey. Items such as garbage, pet food, and sometimes feeding stations for birds and squirrels will attract coyotes into backyards. About three to five pets attacked by coyotes are brought into the Animal Urgent Care hospital of south Orange County (California) each week, the majority of which are dogs, since cats typically do not survive the attacks.<sup>[118]</sup> Scat analysis collected near Claremont, California revealed that coyotes relied heavily on pets as a food source in winter and spring.<sup>[107]</sup> At one location in Southern California, coyotes began relying on a colony of feral cats as a food source. Over time, the coyotes killed most of the cats, and then continued to eat the cat food placed daily at the colony site by people

who were maintaining the cat colony.<sup>[107]</sup> Coyotes usually attack smaller-sized dogs, but they have been known to attack even large, powerful breeds such as the Rottweiler in exceptional cases.<sup>[119]</sup> Dogs larger than coyotes are generally able to drive them off, and have been known to kill coyotes. Smaller breeds are more likely to suffer injury or death.

## Uses

Prior to the mid-1800s, coyote fur was considered worthless. This changed with the diminution of beavers, and by 1860, the hunting of coyotes for their fur became a great source of income (75 cents to \$1.50 per skin) for wolfers in the Great Plains. Coyote pelts were of significant economic importance during the early 1950s, ranging in price from \$5 to \$25 per pelt, depending on locality.<sup>[120]</sup> The coyote's fur is not durable enough to make rugs,<sup>[121]</sup> but can be used for ladies coats and jackets, scarfs or muffs. The majority of pelts are used for making trimmings, such as coat collars and sleeves for women's clothing. Coyote fur is sometimes dyed black as imitation silver fox.<sup>[120]</sup>

Coyotes were occasionally eaten by trappers and mountain men during the western expansion. Coyotes sometimes featured in the feasts of the Plains Indians, and coyote pups were eaten by the indigenous people of San Gabriel, California. The taste of coyote meat has been likened to that of the wolf, and is more tender than pork when boiled. Coyote fat, when taken in the fall, has been used on occasion to grease leather or eaten as a spread.<sup>[122]</sup>

## Tameability

Coyotes were probably semi-domesticated by various pre-Columbian cultures. Some 19th-century writers wrote of coyotes being kept in native villages in the Great Plains. The coyote is easily tamed as a pup, but can become destructive as an adult.<sup>[123]</sup> Both full-blooded and hybrid coyotes can be playful and confiding with their owners, but are suspicious and shy of strangers,<sup>[60]</sup> though there are records of coyotes being tractable enough to be used for practical purposes like retrieving<sup>[124]</sup> and pointing.<sup>[125]</sup> A tame coyote named "Butch", caught in the summer of 1945, had a short-lived career in cinema, appearing in *Smoky* and *Ramrod* before being shot while raiding a henhouse.<sup>[123]</sup>

## Notes

- Respelled US *ky-OH-tee*, *KY-oht* and UK *koy-YOH-tay*, *koy-YOHT*
- The name "cased wolf" originates from the fact that the coyote's skin was historically cased like that of the muskrat, whereas the wolf's was spread out flat like the beaver's.<sup>[30]</sup>

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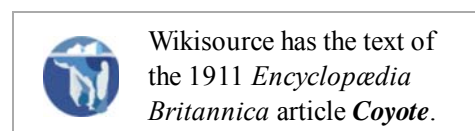
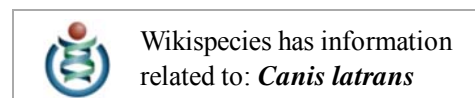
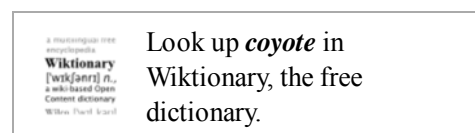
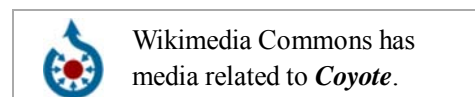
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## External links

- "Canis latrans" ([http://www.itis.gov/servlet/SingleRpt/SingleRpt?search\\_topic=TSN&search\\_value=180599](http://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=180599)). Integrated Taxonomic Information System. Retrieved March 23, 2006.
- Western coyote (<http://wolf.nrdpfc.ca/westerncoyote.htm>), Wolf and Coyote DNA Bank @ Trent University
- View occurrences of "Canis latrans" ([http://biodiversitylibrary.org/name/Canis\\_latrans](http://biodiversitylibrary.org/name/Canis_latrans)) in the Biodiversity Heritage Library.



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