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Wolves

Canis lupus and Allies

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NOMENCLATURE

COMMON NAMES. Gray wolf, timber wolf
SCIENTIFIC NAME. *Canis lupus*
SUBSPECIES. For North America, Hall and Kelson (1959) listed 24 subspecies of *C. lupus*, none described more recently than 1943. It is doubtful whether a systematist revising the wolves today would designate so many subspecies, and possibly none would be recognized. As yet, however, there has been no formal synonymization of any of these subspecific names, and they are still used regularly in literature and in conservation programs. Moreover, it has even been suggested that one subspecies (*C. lupus lycaon*) actually is separable into two distinct entities in Ontario: a larger, "boreal" type in the north and a smaller, "Algonquin" type in the southeast (Kolenosky and Standfield 1975).

Our own studies, involving mainly cranial morphology, indicate that the gray wolf varies in gradual clines over much of North America, and that there are few meaningful places to draw lines separating one kind from another. On the average, the largest skulls of gray wolves are from the northwestern part of the continent and the smallest are from Mexico and southeastern Canada. A relatively abrupt transition in size seems to occur between specimens taken in the main part of Alaska, the Yukon, the mainland Northwest Territories, interior British Columbia, and Alberta, and those taken in the panhandle of southeastern Alaska, coastal British Columbia, and the western conterminous United States. Skulls from the northern arctic islands usually are relatively much broader than those from elsewhere.

EVOLUTION

The gray wolf is a member of the Canidae, or dog family, which is part of the order Carnivora. It is generally considered to be among the most morphologically primitive of the living carnivores, and, along with the coyotes (*C. latrans*), usually is placed at the beginning of systematic treatments of the

order. It is probable, however, that foxes of the genus *Vulpes* represent a more primitive group. Indeed, the genus *Canis* seems to have originated from foxlike ancestors in the early to middle Pliocene.

It is not known when the wolf line became distinct from those of other members of *Canis*, but conceivably this could have occurred by the late Pliocene. Early in the subsequent period, the Pleistocene, there apparently was extensive development and diversification of the wolf line in North America, possibly in response to the extinction of the borophagines, a group of massive dogs that had been present through the Pliocene. The first clearly identifible wolf was *Canis edwardii*, known from a few fossils collected in the southwestern part of the continent. The red wolf (*Canis rufus*), another small, relatively primitive species, and perhaps a direct descendant of *C. edwardii*, also arose in the early Pleistocene, and continued to occupy the southeastern quarter of North America until modern times. Meanwhile, still another branch of this stock of small wolves entered the Old World, where it seems eventually to have evolved into the large gray wolf (*Canis lupus*).

The first of the larger wolves to appear in North America was *Canis armbrusteri*, known from extensive mid-Pleistocene material in Maryland and Florida and which probably occurred all across the continent. In the late Pleistocene the dire wolf (*Canis dirus*) appeared from southern Canada to South America. The largest member of the genus ever to exist, it may have evolved from *Canis armbrusteri*, or developed in South America from the earlier stock of small wolves. Its disappearance about 8,000 years ago probably was associated with the sudden extinction of many of the large herbivorous mammals upon which it preyed. It may also have lost in competition with *C. lupus*, which had invaded North America from Eurasia.

DISTRIBUTION

When European settlement of North America began, the gray wolf occupied the whole continent except the southeastern coastal plain, Baja California, the coastal lowlands of Mexico, and that region south of Estado de

FIGURE 21.1. Past and present distribution of the gray wolf (*Canis lupus*).

FIGURE 21.2. History of the distribution of the red wolf (*Canis rufus*).

Oaxaca, Mexico (figure 21.1). There are no precise records for most of the state of California; the wolf may have been there, but was eliminated at an early time, in association with the development of a major livestock industry by the Spanish in the eighteenth century. The species inhabited the Island of Newfoundland, Vancouver Island, the islands of the Canadian arctic, several coastal parts of Greenland, and most of the islands of southeastern Alaska. It is not known to have ocurred in the West Indies, on the Queen Charlotte Islands, on Kodiak Island, or on Admiralty, Baranof, and Chichagof islands off southeastern Alaska. In historical time the gray wolf occupied all of Eurasia except the tropical forests of southeast Asia. Its range included Ireland, Great Britain, Sicily, Sakhalin, and Japan, but not Ceylon, Formosa, the Philippines, or the East Indies. Human persecution and habitat modification have eliminated the wolf in many parts of the Old World, especially in Europe, and the species has been entirely extirpated in Ireland, Great Britain, and Japan.

The domestic dog (*Canis familiaris*) probably originated over 15,000 years ago from some South Asian population of the gray wolf, and subsequently spread throughout the world in association with people. Some authorities consider the domestic dog to be only a subspecies of *C. lupus*. The wild dingo (*Canis familiaris dingo*) of Australia apparently descended from dogs introduced by the aboriginal human population.

The red wolf once inhabited the region from central Texas and central Oklahoma to the Atlantic, and from the Gulf of Mexico north to southeastern Kansas, from the Ohio Valley, and southern Missouri, the Ohio Valley, and southern Pennsylvania. Lawrence and Bossert (1967, 1975) questioned the specific separation of *C. rufus* from *C. lupus*. For evidence supporting continued recognition of the red wolf as a distinct species, for documentation

of its range (figure 21.2), and for more details on the entire above discussion, see Nowak (1979). A brief discussion of the red wolf is presented separately at the close of this chapter.

DESCRIPTION

Externally the gray wolf resembles a large domestic dog of an unspecialized breed, such as a German shepherd, but usually differs in having relatively longer legs, larger feet, and a narrower chest (Banfield 1974). In addition, the wolf's face can be distinguished by its wide tufts of hair that project down and outward from below the ears (Mech 1970). If a long tail is present on a domestic dog, it generally curls upward posteriorly, but a wolf's tail is straight. Adult wolves, except for some melanistic individuals, have white fur around the mouth, but dogs usually have black fur in this area.

The total length of North American specimens of *C. lupus* usually is about 1,300 to 1,800 mm, of which approximately one-fourth is tail length. Shoulder height is about 700 to 800 mm. Among the adults of any one region, males are usually, but not always, larger than females. Mech (1974) stated that males weigh from 20 to 80 kg and females from 18 to 55 kg. Average weight for males is about 30 kg in southeastern Canada and Mexico and 45 kg in northwestern Canada and Alaska. For more discussion on weight in *C. lupus*, see Mech (1970, 1974) and Young and Goldman (1944).

Wolves are digitigrade, walking so that only the toes touch the ground. There are five toes on the front foot, the first being only rudimentary and not reaching the ground but having a well-developed dew claw. The hind foot has four toes. The claws are nonretractile, blunt, and nearly straight. Young (1944) reported that wolf tracks in the Rocky Mountains averaged 90 mm in

length and 70 mm in width for the front foot, and 82 mm in length and 64 mm in width for the hind foot. In comparison with those of large dogs, tracks of wolves are more elongated, have the front two toe prints closer together, and show the marks of the two front toenails more prominently.

Pelage. The pelage of wolves consists of long, coarse guard hair, mostly measuring 60 to 100 mm, and much shorter, softer underfur (Young and Goldman 1944; Mech 1974). The fur is considerably longer and denser in northern populations. Dorsal hairs generally are longer and darker than those of the underparts. The longest hairs of all, measuring 120 to 150 mm, are found in the mane, a special erectile part of the pelage that extends along the center of the back from the neck to behind the shoulders. Wolves usually have one long annual molt, beginning in late spring when the old coat is shed. Simultaneously, the new, short summer coat develops, which grows through the fall and winter.

The coloration of wolves is so highly variable that it is generally of little value in ascertaining the geographic origin of the specimens. Over much of its range the "gray" wolf may vary in color from pure white to coal black. The usual color is not gray, but is basically light tan or cream mixed with brown, black, and white. Much of the black is concentrated on the back, the forehead tends to be brown, and the lower parts of the head and body are whitish. Light-colored or all-white wolves predominate in much of the northern arctic, but black individuals also are present there. Dark-colored or all-black wolves are relatively common in Alaska and the interior of western Canada. Distinctly white or black individuals seem to have been less common in the conterminous United States, although white wolves were reported from the Great Plains and black wolves from some of the eastern forest areas. Standfield (1970) stated that, in Ontario, wolves to the north of Lake Superior varied in pelage from white to black but wolves to the east and southeast of Lakes Superior and Huron were invariably gray brown.

Certain specialized hairs are present in the pelage of wolves. Elongated whiskers, or vibrissae, on the muzzle are organs of touch. A group of stiff hairs surrounds the precaudal gland located on the back about 70 mm above the base of the tail. These hairs usually are tipped with black, even in animals that otherwise are completely white (Mech 1970).

Skull and Dentition. The skull of a gray wolf usually has a greatest length of 230–290 mm and a zygomatic width of 120–150 mm. Recently, the largest skulls of *C. lupus* on record, one measuring 305 mm in greatest length, were found in Alberta (Gunson and Nowak 1979). A wolf skull has an elongated rostrum, a broadly spreading zygomata, a heavily ossified braincase, and usually a pronounced sagittal crest (figure 21.3). A skull of *C. familiaris* of equivalent size can readily be distinguished by its much more massive, steeply rising, frontal region (one usual result of which is a higher orbital angle; see Mech 1970), and its relatively smaller teeth. The normal dental formula for all

FIGURE 21.3. Skull of the gray wolf (*Canis lupus*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

members of the genus *Canis* is (3/3, 1/1, 4/4, 2/3) x 2 = 42. The incisors are relatively small, and the canines are large, with an exposed dorsoventral length of about 26 mm in *C. lupus*. The fourth upper premolar and the first lower molar form the carnassials.

The molars of wolves retain a flattened or chewing surface, but not to the same extent as in the coyote

(*C. latrans*), which depends more on vegetable matter in its diet.

The red wolf resembles the gray wolf in most respects, but is smaller in average size. Total length usually is about 1,300–1,600 mm, and weight usually is 20–35 kg for males and 16–25 kg for females. It reportedly has relatively longer legs, larger ears, and shorter fur. Its color is not really red, as in a red fox (*Vulpes vulpes*); it is much like that of most *C. lupus*, though perhaps sometimes with a stronger rufous tinge to the flanks and limbs. Some gray wolves, however, also are reddish. A dark-colored or black phase of *C. rufus* apparently was locally common in the heavily forested parts of the range of the species.

PHYSIOLOGY AND GENETICS

The internal anatomy of the gray wolf is not known to differ substantially from that of domestic dogs as described by Miller et al. (1964). The digestive system of the gray wolf was discussed in detail by Mech (1970), who commented on its efficiency in absorbing large amounts of meat while ridding itself of indigestible matter such as hair and bone. He also observed that malnutrition probably is not generally a direct threat to the survival of the wolf.

Serological and karyological studies have not yet disclosed a reliable means of distinguishing among *C. lupus*, *C. rufus*, *C. latrans*, and *C. familiaris*. All have a diploid chromosome number of 78, and the chromosomes appear identical in each species (Chiarelli 1975). Hybridization appears to occur relatively readily in the genus *Canis*. Viable hybrids have been reported between *C. lupus* and *C. familiaris*, *C. lupus* and *C. latrans*, and *C. rufus* and *C. latrans* (Gray 1972; Nowak 1979). Large-scale hybridization in the wild has occurred between the gray wolf and the coyote in southeastern Canada, and between the red wolf and the coyote in the south-central United States, and has resulted in the modification of populations of *Canis* over large areas.

REPRODUCTION

Mech (1974) has summarized the breeding data on wolves, and most of the following is based on his discussion. Wolves gain sexual maturity in their second year, but often do not breed until their third year. It is commonly thought that wolves mate for life, and in captivity wolves do demonstrate strong and longlasting mate preferences. The receptive period of the female may be anytime between January and April, depending on the latitude. Courtship takes place between pack members or between lone wolves that pair during the mating season. The female is in estrus for 5 to 7 days and blood may flow from the vulva for a few days to a few weeks before estrus. Copulation is in the typical canid fashion, with the bulbous base of the male's penis locking into the female's vaginal sphincter, the tie lasting anywhere up to 30 minutes. The gestation period is 63 days. An average of 6 young (1 to 11) are born blind and helpless, usually in a shel-

tered place in a hole, rock crevice, hollow log, or overturned stump.

Development of the Pups. The female stays near the young for several months, while the male and other pack members hunt and feed them. The pups' eyes open at 11 to 15 days, and weaning takes place at about five weeks. After about eight weeks, the pups are moved up to an aboveground nest (the "rendezvous site"), where they romp and play over an area up to 0.4 hectare in size. The pups continue their development over the summer and may join the adults of the pack in their travels by October, at which time they are almost of adult size. Adult teeth replace milk teeth in the 16th to 26th month.

From the third week of their lives, wolf pups begin appearing outside the den, romping and playing (Young and Goldman 1944). This marks the beginning of their period of socialization, during which they develop behavior patterns and emotional attachments to places and other wolves (Scott 1967). Play fighting and agonistic behavior during this period eventually help establish the dominance relations that the wolves will develop later.

The period of socialization is also important to the formation of emotional bonds. These emotional attachments are the basis for the formation and continuation of the pack. This process takes place during a period when members of a litter begin following one another and acting as a group (Mech 1970).

Feeding behavior of pups begins to change at this time. At first, the young are forced to nurse while standing, follow the mother around the den, and eat the food regurgitated by adults. Feeding on these semiliquid disgourgements eventually leads to weaning, which is a more gentle process in wolves than in domestic dogs (Ginsburg 1965). Also during the period of socialization, wolf pups learn to run, climb, jump, and play in adult patterns, and the beginnings of predatory behavior can be observed. Mech (1970) reported that his captive male pup snapped "viciously" at raw meat offered to him when he was 34 days old, and chewing and tugging at soft objects was apparent before this age. By the 10th week of life, a wolf pup will menacingly shake mops, and will even chase small animals.

Based on his observations of wolf pups, Mech (1970) felt that the species does not have an inborn tendency to kill, but rather is born with certain behavior patterns that allow it to learn to kill. Apparently, both imitation of killing behavior of the adults and association of killing with eating are important steps in the learning process. This learning process continues on into what Scott and Fuller (1965) call the juvenile period, from about the 12th week to sexual maturity. During this period, the wolf pups do some limited mouse hunting (Murie 1944), gradually replace the milk teeth with permanent dentition, and grow to adulthood.

At about the middle of the juvenile period, 10 months of age, the pups are the size of adults and are participating in the hunt, but the learning of when,

where, and how to hunt appears to be a continuing process throughout the life of each animal (Mech 1970). The maximum life expectancy of wolves is 16 years, although a 10-year-old wolf can be regarded as a very old animal.

ECOLOGY

Gray wolves do not seem particular about habitat. They originally occurred in arctic tundra, taiga, plains or steppes, savannahs, and hardwood, softwood, and mixed forests. Examination of their former distribution reveals that gray wolves occupied nearly the entire land surface of the two northern continents (Mech 1970). Young and Goldman (1944) doubted that any other wild land animal ever had a greater range. (It now seems likely that one did; if all Pleistocene lions represented *Panthera leo*, as thought by Hemmer [1974], that species would have occurred throughout Africa, Eurasia, North America, and South America.)

The only major terrestrial barriers to wolves appear to have been the hot, dense forests of southeast Asia and the neotropics, and the hot, dry deserts of northern Africa and Baja California. Wolves even have freely crossed pack ice to occupy Greenland and all the larger islands of the Canadian arctic. Rather than on land form, climate, or vegetation, the presence of wolves seems to have depended on the availability of suitable prey.

Dens. Unlike many mammals, wolves do not make regular use of shelters. A den is constructed only for a female to give birth and care for her young for about two months. Dens usually are located on slopes, ridges, or other high ground, and near a source of water. A typical den is a hole with an entrance 0.36–0.63 meters in diameter, and a tunnel extending 1.3–4.5 m into the ground. There may be several entrances, and the tunnel often curves upward, downward, or sideways. At the end of the tunnel is a nesting chamber that measures about 1.5 m long, 1.2 m wide, and 0.9 m high. No bedding material is used. Wolves may also den in such places as abandoned beaver lodges, hollow logs, rock crevices, or merely surface depressions (Mech 1970, 1974; Stephenson 1974).

Dens may be reused year after year, but occasionally the young are shifted from one den to another during a single season. When the pups are about 8 to 10 weeks old the use of a den ceases, and the young are then brought to what is called a rendezvous area. In the Great Lakes region such sites usually are near a pond or bog, and consist of a system of trails, beds, and areas in which vegetation has been flattened, presumably by playing of the pups. Reported sizes of rendezvous areas vary from about 0.4 to 1 km long. The pups remain in these areas while the pack hunts. A succession of rendezvous sites are used, generally until the fall, when the young have grown sufficiently to accompany the adults on their travels. The reported period of occupation of each site varies from 6 to 59 days (Joslin 1967; Mech 1970, 1974; Van Ballenberghe et al. 1975; Peterson 1977).

Seasonal Activity. The wolf generally has two main types of wanderings: (1) those that center around the den and the pups from April to late fall, and (2) those that take place during the rest of the year, when the animals roam widely. Generally, there is a day/night activity pattern in the summer, with the animals staying close to the dens during the day and wandering out to hunt during the late afternoon or early evening; they usually return to the den by morning. Perhaps the primary reason for night hunting during the summer is the wolves' sensitivity to heat. The animals generally spend their days trying to keep cool, seeking out shady areas and seldom staying in direct sunlight for even short periods. Wolves pant a great deal in hot weather and quickly become overheated even with slight exertion; their preference for cooler nighttime travels therefore is readily understood (Mech 1970).

In summer, in some areas, such as the tundra, wolves may travel as much as 30 km from the den site to obtain food, a round trip of 60 km or more; in the forested areas, distances traveled are usually far less. This is probably because the food supply is more widely and unevenly distributed on the tundra. Wolves wander along waterways, dirt roads, game, cattle and sheep trails, ridges, and shorelines during their regular hunting activities. When pups are young, the movements of the adults are shorter and less frequent than later in the year. In May, June, and July, the average distance traveled during the hunt may be as little as 1.5 km, whereas later the animals may range out to 3 or 4 km a day. Of course, animals without pups or packs without reproducing members are not restricted as closely to dens and wander more widely than packs with pups.

In the fall, wolf pups abandon their rendezvous sites and join the adults on hunting forays. Thus, the pack no longer needs to restrict its wandering to small areas near the dens. During the winter then, the packs wander freely and widely over vast areas, tracking their prey wherever it may flee. Generally, winter hunting is nocturnal, but often the wolves may travel for days on end, resting only at periodic intervals to recover their strength. In winter, wolves use game trails, roads, ridges, and sometimes even highways to avoid the deep snows that would hamper them in any hunting or moving activity.

In winter, movements of wolves are surprisingly lengthy and rapid. In Ontario, seven wolves moved 65 km in no more than 20 hours and during that time killed and ate one large and one small deer. In Minnesota, a pack traveled 56 km overnight on a chain of frozen lakes, and in Alaska, a pack moved 72 km during no more than 24 hours. Mech (1970) reported that on Isle Royale, the fastest long-distance move he observed was 72 km in 24 hours, mostly along well-established shore routes. The greatest movement of a wolf on record covered a straight line distance of 670 km during an 81-day period in central Canada (Van Camp and Gluckie 1979).

In northern areas, where the primary source of food for wolves is caribou (*Rangifer tarandus*), the wolves appear to be migratory and to follow the

caribou as those animals travel throughout the year. Kelsall (1968) stated that in the Canadian tundra the tracks of wolf packs have been followed in a straight line for distances of 160 km one way, moving seasonally from tundra to forest or vice versa. Sometimes they followed caribou trails and at other times they headed for the caribou herds with "uncanny accuracy from directions not used by the caribou." In Alaska, wolves are known to accompany migrating caribou herds. After making a kill, they remain with the carcass until it is devoured, after which they may rapidly travel 40 to 65 km to catch up with the moving herd. On the other hand, in areas where prey is not migratory and is numerous, wolves will remain in a specific area the year around.

In areas with high mountains and heavy snowfalls, such as in the Rocky Mountains, wolves may move down from higher elevations into the valleys during winter. This shift to lower elevations, however, does not appear to be an actual migration on the part of the wolves. Probably it is a response to the difficulty they experience in maneuvering in the deep snow, and the fact that most game on which they feed has migrated to lower elevations. During this winter period when the wolves are in the valleys at the lower elevations their movements may be more restricted than usual and their entire range may be no more than 26 km² per wolf. In the spring and summer, when the snow begins to melt and deer and other game move up to their summer ranges at higher elevations, the wolves follow them and resume their wider-ranging hunting activities until they are again restricted by the birth of pups (Mech 1970).

FOOD HABITS

The wolf is a meat-eating animal, and its entire digestive system is adapted to a carnivorous diet. Typically, it consistently feeds on large prey such as deer or caribou rather than on smaller animals such as rabbits (*Sylvilagus* sp.). The large size of the wolf itself, combined with its habit of traveling in packs, makes it perfectly adapted to feed on larger species of prey.

Studies by Murie (1944) on Mount McKinley in Alaska, Cowan (1947) in the Rocky Mountains of Canada, Thompson (1952) in Wisconsin, Mech (1966) on Isle Royale in Michigan, Pimlott et al (1969) in Algonquin National Park, Ontario, and Van Ballenberghe et al. (1979) in northeastern Minnesota, showed that 59 to 96 percent of the food items consumed by wolves were animals the size of beavers (*Castor canadensis*) or larger. The most frequently taken prey were white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), Dall sheep (*Ovis dalli*), bighorn sheep (*Ovis canadensis*), and beaver.

Cowan (1947) found that in the Canadian Rockies, 80 percent of the food consumed by wolves was big game and only 18 percent consisted of rodents. In northern Wisconsin, Thompson (1952) reported that 97 percent of 425 wolf scats collected were comprised of deer remains, while only 9 percent of the scats contained snowshoe hares (*Lepus townsendii*). In northern Minnesota, Stenlund (1955) found that white-tailed deer comprised 95.5 percent of the total volume of wolf stomach contents. He also found that small animals were more often consumed in summer than in winter. Pimlott et al. (1969) reported that deer were the primary prey of wolves in Algonquin Park, while moose and beaver were of lesser importance. Moose were the only prey for wolves on Isle Royale in Michigan. Mech (1966) determined that the wolf and moose populations were in dynamic equilibrium, with wolves culling out the weak and infirm moose and thus stimulating moose reproduction. In areas where caribou are abundant, Banfield (1954), Kelly (1954), Kelsall (1960), and Kuyt (1972) found that the wolves feed almost exclusively on the caribou. Kuyt also found that wolves prey on arctic fox (*Alopex lagopus*), red fox (*V. vulpes*), arctic hare (*Lepus arcticus*), arctic squirrel (*Spermophilus undulatus*), microtine rodents, birds, eggs, fish, and insects, but to a much lesser extent than they prey on caribou.

According to Mech (1970), domestic animals usually eaten by wolves in North America include cattle, sheep, horses, swine, dogs, and cats. He stated that these species have evolved under constant protection by humans and that they are unable to protect themselves well. Therefore, wherever they occur in the vicinity of wolves they fall easier prey than animals that evolved with the ability to protect and defend themselves.

The teeth of wolves are designed to tear and cut large chunks of meat and to crush and crack bone. Wolves bolt their food and make little attempt at chewing. The size of pieces of prey swallowed by a wolf is impressive. In Alaska, one wolf's stomach contained a caribou ear, tongue, lip, two kidneys, liver, and windpipe, plus hair and large chunks of meat (Kelly 1954). Each wolf can consume almost 9 kg of meat at a feeding (Mech 1970). The food is digested quickly, so the animal probably eats several times a day when large amounts of food are available. Mech (1970) several times saw packs of 15 or 16 animals on Isle Royale consume all the edible parts of a moose calf weighing about 135 kg within 24 hours. On one occasion he saw the pack finish about half of a mature moose in less than 2 hours, which meant that each wolf consumed about 9 kg of meat in 1.5 hours. Mech (1970) estimated that a healthy, active wolf would need to consume a minimum of 1.7 kg of meat a day in order to maintain itself. Average reported consumption rates were 2.5 to 6.3 kg of moose per wolf per day (Mech 1974).

Although wolves can eat enormous amounts of food in very short periods at frequent intervals, the species is also well adapted to go for long periods, sometimes several days, without food. Mech (1966) reported that a pack on Isle Royale once went at least 95 hours without eating anything except hair and bones that they might have gleaned from old kills. Young and Goldman (1944) mention a wild male wolf that, when kept in captivity, did not eat anything for 7 days, but on the 8th day gorged itself. In the Soviet Union, it has

been reported that a wild wolf went without food for 17 days, the longest recorded fast for a wolf (Makridin 1962). In the light of the evidence, Mech (1974) thought that wolves can probably fast for two weeks or more while searching about for suitable prey, and then gorge themselves on enormous quantities in order to prepare for another period of fasting. The benefit of such a digestive system is obvious in a large predatory animal like the wolf.

Hunting. Wolves spend almost their entire waking time either eating or hunting. After finishing a meal, wolves begin almost immediately to search for new prey. Mech (1970) found that on Isle Royale the average distance traveled by wolves between kills was 36 km. The pack could show interest in a new kill within 35 minutes of abandoning the old one. They are apparently continually ready to hunt and have no special hunting grounds or behavior. The animals simply travel around and whenever they find a potential prey they attack it. In some regions, they may have to travel through vast areas where game is scarce, but they move through these areas rapidly and spend most of their time wandering and hunting in areas with prey.

Wolves have three main methods of locating prey: direct scenting, chance encounter, and tracking (Mech 1970). Of these three, direct scenting is the most often used. In 51 hunts on Isle Royale in which hunting methods could be determined, wolves used direct scenting in 42 cases. Usually the wolves could scent moose when within 300 m downwind, but on one occasion a cow and its calves were scented about 3 km away. Observations have shown that deer may also be located by odor. When the wolf packs are traveling and detect the scent of prey, the leaders stop and all animals stand alert, looking toward the source of the scent. Then they veer abruptly and head directly toward the prey.

Wolves locate prey through chance encounter less often than by direct scent. Most chance encounters would take place only in areas where prey species are very abundant. Thus, in areas inhabited by deer, which normally occur in high densities, chance encounters would be especially important (Mech 1970). Mech observed several hunts in Minnesota where deer were located in this fashion. Evidence suggests that chance encounters play a major role with wolves that prey on Dall sheep in Mount McKinley Park (Murie 1944). Banfield (1954) reported that on the Canadian tundra, wolves "patrol" an area and flush out caribou at close range.

In 9 of 51 hunts observed by Mech (1970) on Isle Royale, tracking played the major role in obtaining the prey. Observations indicate that wolves use this method only when the tracks are very fresh; older tracks are generally ignored.

Once the wolves have located suitable prey, either by direct scenting, chance encounter, or tracking, they stalk it, usually approaching the animal in the same fashion. That is, they slowly close the gap between themselves and the prey, becoming more excited and quickening their pace the closer they get. They wag their tails and peer straight ahead, but they continue to show restraint and move quietly and cautiously. In this way the wolves may move to within 30 m of the prey without being observed (Crisler 1956; Mech 1970). Once the quarry has spotted the stalking wolves, it may either stand its ground and fight or bolt and try to escape. Usually, only very large prey such as moose or bison will stand and fight, in which case they often fend off the attackers. In fact, wolves seem quite hesitant about attacking any animal that does not attempt to run to safety (Mech 1970). If the prey bolts, however, the wolves immediately give chase in a maneuver that Mech terms the *rush*. This is the most crucial part of the hunt, and often the attacked animal succeeds in escaping without the wolves even getting close to it. If, however, the wolves do overtake the fleeing prey, they attack by biting on the rump, flanks, and shoulders; rarely, if ever, do wolves hamstring any animal they attack. Occasionally, wolves pursue their quarry many kilometers before giving up or launching their final attack. Usually chases are much shorter, generally 1 km or less (Mech 1970).

Upon overtaking and killing the quarry, all the wolves in the pack immediately begin feeding, and within a short time are finished and ready to hunt again. The only exception seems to be when female wolves are restricted to dens during the pupping season. In such cases, all the wolves in the pack apparently help feed the female and young. Murie (1944) reported on at least three wolves that carried food back to a mother in Mount McKinley Park. They took some of it directly to the den, but cached the majority of it a considerable distance away, some as far as 0.8 km distant. On three nights, an adult female other than the mother stayed at the den while the mother accompanied the pack on the hunt. The males in this pack also showed much interest in the pups.

Predator-Prey Relations. The effects of wolves on their prey fall into three categories: (1) culling of inferior animals; (2) the control or partial control of prey populations; and (3) the stimulation of productivity in herds of prey (Mech 1970).

There is little question that wolves play a major beneficial role in removing sick and inferior animals from a herd. Wolf predation generally is selective, resulting in the removal of very young, very old, sick, wounded, crippled, and other infirm individuals. These animals contribute little to herd dynamics and their removal would increase the amount of food, space, and cover for the more productive members of the herd. The diseases of hoofed animals are numerous. Internal and external parasites also plague the prey of the wolf. In some cases, wolf predation might help reduce parasites and diseases by culling the individuals that carry them.

Concerning the wolf's control or partial control of prey populations, the evidence is less clear. The problem is an extremely complex one and is discussed in detail by Stenlund (1955), Pimlott (1967), and Mech (1970). Many factors are involved and interrelated, including prey density, predator density, weather,

TABLE 21.1. Density per square kilometer for various North American wolf populations

Location	Area (approx. km²)	Density of Wolves (approx. km²/wolf)	Authority
Isle Royale, Michigan	546	18–26	Mech 1966; Jordan et al. 1967
Algonquin Park, Ontario	2,600	26	Pimlott et al. 1969
Ontario	26,000	260–500	Pimlott et al. 1969
Minnesota	6,475	26	Olson 1938
Minnesota	8,660	44	Stenlund 1955
Minnesota	1,865	24	Van Ballenberghe et al. 1975
North Central Brooks Range	9,120	170–320	Stephenson 1975
Mt. McKinley Natl. Park, Alaska	5,200	130	Murie 1944
Mt. McKinley Natl. Park, Alaska	3,900	85	Haber 1968
Unit 13, Alaska	52,000	130	Rausch 1967
Tanana Flats, Alaska	18,200	90	Stephenson 1977
Southeast Alaska	19,500	65–100	Atwell et al. 1963
Saskatchewan		104–216	Banfield 1951
Northwest Territories	1,248,000	155–312	Kelsall 1957
Western Canada	1,500	229	Carbyn 1974
Baffin Island	4,680	312	Clark 1971

available browse, and other mortality factors. Studies of wolves on Isle Royale, in Superior National Forest, and elsewhere indicate that they do not play a major part. However, Pimlott (1967) and Mech (1970) believe that wolf predation may have been the main limiting factor on most, if not all, big game species before people so greatly disturbed the habitat.

Prey herds with an adequate food supply that have had old, sick, and debilitated members removed by wolf predation could be expected to reproduce most vigorously. The only place, however, where such a situation has been examined closely is on Isle Royale, Michigan. There, moose inhabited the island for decades before the wolf arrived, so comparison can be made on reproduction prior to and after the advent of the wolf. Mech (1970) reported that the only figure for which enough data are available on moose reproduction on Isle Royale is the twinning rate. This is probably the most sensitive indicator of productivity in a moose herd. Before wolves arrived on Isle Royale, about 1949, very few twin calves were observed. In 1929 and 1930, only 6 percent of 53 cows had twins. However, in 1959, after the wolves had cropped the moose herd for 10 years, the twinning rate was about 38 percent. This rate is much higher than that for any other moose population in North America. Thus, although the data pertain to only a single population and to only one index of fertility, it seems likely that wolves do stimulate productivity in herds of larger prey.

POPULATION DYNAMICS

One wolf per 26 km² constitutes a high density; much lower densities are common over large areas (Pimlott 1967). Pimlott felt that one wolf per 26 km² represents the saturation point beyond which wolf populations cannot exist. However, Kuyt (1972) reported that wolf densities can compress in winter in some parts of Northwest Territories (Mackenzie) to about one wolf per 10 km². Further, Van Ballenberghe (1974), working in Superior National Forest, found a 550-km² area of wolf pack territories in which the densities reached an average of about one per 13.8 km². In these instances, however, it should be noted that prey densities were extremely high; caribou averaged 68 per about 2.5 km² in their Canadian wintering areas. Deer may have averaged as high as about 166 per 2.6 km² in one of their winter yards in Superior National Forest. Thus, as Mech (1974) concluded, while it is true that average wolf densities do not exceed about one wolf per 26 km² (and are usually far lower than this), during certain periods of exceptionally high prey concentrations, wolf densities may almost double. The highest density ever reported for wolves was about one per 8 km², on Coronation Island, Alaska (Merriam 1964), and the lowest was one wolf per 260 to 500 km², in Ontario (Pimlott et al. 1969). Table 21.1 shows the density per square kilometer for various North American wolf populations.

Home Range Size. The term *home range*, as generally used by wolf biologists, means the area of land either enclosed by the runways of a particular pack or available to use by the pack, given its usual travel habits (Mech 1970). In the summer, tundra wolves are known to range as far as 30 to 35 km from the den. Mech (1970) speculates that if the den is in the center of a pack's range and the wolves forage in several directions, the area of the range could be as great as 3,100 km². If, however, the den is only on one edge of the range, the area would approximate only 390 to 780 km². Although home ranges must vary widely, it is evident that on the tundra most of them must be relatively extensive.

Little is known about the summer ranges of wolves in the forested regions, but evidence indicates that they are considerably smaller than in the tundra. Studies by Joslin (cited in Mech 1970) indicated that the range of one pack in southern Ontario was at least 20 km² in one year and 18 km² in another. Mech felt that these figures were probably too low and that the

actual range was far larger. Joslin also believed that the total summer range of one Ontario pack that he studied may have been as large as 65 km² (from Mech 1970).

Wolves have a larger home range in winter than in summer. Various studies indicate a range of from about 94 km² for a pack of 2 animals (in Minnesota) to about 13,000 km² for a pack of 10 animals (in Alaska) (Mech 1970). Reduced to a km²/wolf basis, the range would be from about 47 km² per wolf to 1,300 km² per wolf. There is much room for skepticism with regard to published figures of wolf home ranges; such ranges may actually be larger than the published figures indicate.

BEHAVIOR

Social Life and the Pack. Wolves are highly social animals and almost always live in packs. The pack is the basic unit in the social structure and consists of a group of individual wolves that hunt, feed, travel, and rest together. Members of a pack are loosely associated with each other, but the bonds of attachments of individuals living within the pack are strong. Pack size is highly variable. The highest number of wolves recorded in a pack was 36 animals observed by Rausch in south-central Alaska (Mech 1967). Other large packs of 20-21 animals have been observed on occasion in Alaska. Mech (1970) spent several weeks tracking a pack of wolves on Isle Royale, Michigan, that numbered 15-16 animals. However, most wolves associate in packs of 8 animals or less.

The social composition of wolf packs is not clear. It has generally been assumed that the pack contains a breeding pair and their pups, yet many packs contain several adults in breeding condition. Mech (1970) listed the following basic facts about wolf packs:

1. Populations of wolves consist of packs occupying adjacent and sometimes overlapping regions of range.
2. Most packs contain fewer than eight members.
3. Temporary associations of two or more packs sometimes occur, forming a very large group (this is quite rare, however).
4. Several instances are known of packs chasing nonmembers away.
5. In some cases, a pack has accepted one member of a different group and rejected another member.
6. Strong bonds are needed to hold a pack together; if there were no bonds, each wolf would go its own separate way.
7. Most packs include a pair of breeding adults, pups, and extra adults that may also breed.

It appears that packs are held together by strong bonds of affection. These bonds might develop when two lone adult wolves come together to mate. The courtship of wolves is a lengthy ritual. During this period, the pair may develop an attachment for each other that extends beyond the breeding period and keeps them together as the nucleus of a pack. Pups born to the pair develop the bonds of affection for each other at an early age, generally before five months of age (Mech 1974). Thus, wolf packs may be composed entirely of related individuals. Mech (1970) presented the following theory of pack formation, which is consistent with present knowledge of pack composition and behavior, and explains conflicting observations: the basic component of the pack is the breeding pair, and a pack is first formed when a lone male and female mate in late winter. The pack is added to by the first litter (often as many as six pups), which in order to learn to hunt must stay with the parents at least through the first winter. Because the pups do not mature until they are two years old, there would be no sexual conflicts during the next breeding season when the original pair mate again. As the first pups advance into their third year, rivalries may develop between them and the original pair, or strong sexual attachments may develop between them and strange wolves, so that some of them leave the pack to form new packs. In some instances, however, littermate matings might occur and these wolves would stay with the original pack and increase its size.

The next stage at which a pack might break up is during the third denning period, three or four weeks before the original pair give birth to their third litter (Mech 1970). Each mated pair might separate from the pack, dig its own den, and raise its own young apart from the rest of the pack. This might develop new bonds and help to break old ones, thus forming a new pack nucleus. When this new pack met with the old one, it would recognize its former pack mates. The new pack might travel together with the old temporarily, but soon would separate to develop its own travel routes and hunting areas, particularly in times of food shortages.

Dominance and Leadership. Within any pack of wolves, there is a strict, ridgidly enforced social structure based on dominance. There are two dominance orders within each pack, a male order and a female order. Dominance within these orders is linear in nature, with the highest-ranking male being dominant over the next highest ranking, and so on down the order to the least dominant male. A similar order is found among the females. Generally, the highest-ranking male, known as the alpha male, is dominant over all other animals in the pack, males and females, and is the recognized leader. The most dominant female, known as the alpha female, is dominant over all females in the pack, but is subordinate to the alpha male. She may, however, be dominant over some of the other males in the pack but generally males dominate females. The alpha male and female usually are the original founding members of the pack.

The dominance shown by the alpha animals and other high-ranking wolves was described by Mech (1970) as a kind of "forceful initiative." When a situation does not require initiative, dominance may not be shown, for example, when a pack is resting. However, dominance comes into play when the pack is feeding, mating, seeking favored space, encountering strange wolves, or in other such active or competitive situations.

There are two main aspects of dominance in a wolf pack: privilege and leadership (Mech 1970). Privilege involves the dominant wolf's taking the initiative in any competitive situation and claiming whatever it desires. Thus, the dominant wolf has the first choice of food, bedding sites, and mates. Usually none of the other members of a pack disputes the claims of a dominant wolf, although two animals closely related in rank may compete. There are some exceptions to the privileges of a dominant animal, however, notably when a female gives birth to young. A normally subordinate female, after its pups are born, may take an aggressive attitude toward a dominant male and drive it away. Schoenberner (1965) stated that the only time an alpha male is dominated by a female is when the female is caring for a newborn young.

Leadership is probably the most important aspect of pack dominance. Obviously no pack could exist as a unit if each individual member decided for itself when to rest, hunt, or seek refuge. Some members of the pack must take the initiative in these activities, and dominance appears to be the major factor in determining leadership. Generally, in any pack, the alpha male is the most highly motivated animal and serves as leader of the pack. Leadership is evidenced in wolves when they are attacking prey, traveling overland, or waking from a long nap (Mech 1970). Highly dominant males, other than the alpha male, may at times play a leadership role in the pack, but females rarely do.

Leadership also involves a guarding function in the pack. Murie (1944) described a case where the leader of a pack remained alert one day while other wolves rested, and then suddenly led an attack on a strange wolf that approached. On another occasion, this same wolf was the most aggressive in defending the pack's denning area from an invading grizzly bear (*Ursus arctos*).

As yet, the manner in which an alpha male controls the pack is not known. It could be an autocratic type of leadership in which the leader dictates the activity and the other members follow the lead without protest. Or, the leadership could be democratic, with the alpha male taking its cue from the behavior of other pack members. A third possibility is that the leadership could combine elements of both autocracy and democracy.

Territoriality. Mech (1970) accepts the definition of an animal's territory as being the area that the animal will defend against individuals of the same species. Defense of this area is the main difference between "territory" and "home range." With wolves, it appears that packs are territorial, at least to the extent that their territories include most of their hunting and traveling areas. Information on territoriality in wolves is scanty and somewhat conflicting. Data on the Isle Royale population shows that the largest pack used the entire island in winter, but concentrated its activities in about one-half to one-third of the area (Mech 1966). Two smaller packs confined their movements to the part of the island used least by the large pack. Most

information on territories of the Isle Royale packs pertains to winter, but limited summer observations suggest that the packs are spaced about as they are in winter. In Ontario, Joslin (1966) found summer ranges of packs to be separate, with no overlap of ranges between packs. However, Van Ballenberghe et al. (1975) felt that territories would generally be entirely discrete only when minimum territory size is approached, probably because of the greater ease in patrolling small territories.

Howling and Communication. Wolves communicate with each other in a great variety of ways. They may posture or position themselves in various poses to indicate aggression or subservience. They whimper, growl, or utter other sounds in response to fear, pleasure, or pain. The ears may be held erect or flattened against the head, the tail wagged or held stiff, hairs erected or laid flat, all depending on the mood or specific situation in which the animal finds itself.

The wolf whimper is a high, soft, plaintive sound similar to that uttered by domestic dogs; Joslin (1966) considered it to be a submissive or friendly greeting sound. Growling, on the other hand, seems to be uttered primarily in aggressive situations and is a threatening, unfriendly sound. The barking of wolves is deep, guttural, and coarse (Mech 1970). It is apparently basically an alarm call given when other animals impose on a pack's territory (Joslin 1966).

The most commonly heard wolf sound is the howl, a long, low, mournful moan (Mech 1970). A wolf pack may howl at any time of day and any time of year. A single wolf may have a howling session (Joslin 1966). When a pack performs, one wolf begins the howling, and after its first or second howl other animals join in. Each animal starts by itself, beginning with long, low howls and working up to a series of shorter, higher ones. Such a howling session lasts 85 seconds on the average, and is often followed by a repeat performance. All the functions of howling are not yet known. Crisler (1956) believed that howling, like a community sing, is a happy, social occasion. An important function of howling seems to be as an aid in assembling the pack (Mech 1970). The advantage of a method of assembling scattered pack members is obvious, and it is easy to see how this function could have evolved from social gratification. Mech (1970) believed that much of the howling of wolves actually represents the assembling of pack members after a chase. Often wolves get separated during the hunt, and on such occasions one animal may climb a ridge and howl to attract other pack members to it. Other possible adaptive functions of howling are to advertise and maintain territories (Harrington and Mech 1979), to identify individuals, and to supply information about behavior, such as whether the animal is lying down, walking slowly, or pacing (Mech 1970).

One of the most important expression centers for the wolf is the head. In general, teeth bared, open mouth, wrinkled and swollen forehead, and ears erect and pointed forward indicate a full threat by a dominant wolf. Subordination is indicated by a closed

mouth, a smooth forehead, eyes closed to slits, and ears drawn back and held flat against the head.

Another important communicating organ for the wolf is the tail. A threatening wolf raises the tail above the level of the back; a submissive wolf holds the tail low, sometimes tucked between the legs. Loose, free tail wagging usually indicates friendliness, while tight, abrupt wagging of the tail tip can often be associated with aggression.

MORTALITY

Wolves are subject to a great many diseases, of which parasites, both internal and external, are a major cause. Some of the endoparasites that affect wolves are various species of fluke, tapeworm, roundworm, and thorny-headed worm. Lice, tongueworms, fleas, ticks, mange mites, mosquitoes, deerflies, horseflies, black flies, and stable flies are some of the external parasites that attack wolves.

Rabies is the most important disease in wild populations of wolves (Mech 1970). Whether rabies is important in control of wolves is uncertain. Cowan (1949) felt that rabies might play such a role in limiting the number of foxes and possibly wolves as well. Rausch (1958), however, concluded that there is simply not enough known about canine rabies to determine whether it is important in the control of boreal populations of carnivores.

Distemper is another viral canine disease that may occur among young wolves in captivity (Gross 1948). However, Rausch (1958) and Mech (1970) report no cases known to them of distemper in wild populations of wolves. Other diseases that have been reported in captive wolves range from liver and thyroid cancer to bladder stones and chronic nephritis, but the prevalence of these disorders in wild populations is not known.

Other factors that may play significant roles in wolf mortality and possibly in control of populations include injury and accidents, malnutrition, social stress, and persecution and exploitation by humans.

ECONOMIC STATUS

Wherever the wolf occurs, it has generally been feared, hated, and destroyed; people seem always to have been the most relentless and determined foe of the wolf whenever the two species occurred together. Generally, people have killed wolves for three reasons: (1) wolf fur is durable and warm and has been sought for clothing in some areas; (2) the wolf is a large, aggressive animal and people generally have feared for their own personal safety when living in proximity to wolves; and (3) the wolf is a known predator on domestic livestock in some situations.

By far, hatred of the wolf as a predator on livestock has been the major factor in human persecution of the species. In general, wolf fur has never been widely appreciated as a major article of clothing. Some American Indian tribes used wolf fur to make shoes, caps, and robes, but deer and bison hides were gener-

ally of much greater importance to them. Europeans and American settlers used wolf fur as trimming on their garments, and because of its durability, warmth, and frost-free qualities, this is its primary use today. However, persecution for its hide has been, and continues to be, only a minor factor in the decline of the wolf.

Of more importance has been the fear that the wolf is a serious threat to human safety. At one time the wolf was so dreaded in some parts of Europe that merely mentioning its name was considered a crime (Ricciuti 1978). It is believed that as many as 3,000 people have been killed by wolves in Europe over the past 500 years. Many terrible tales are told in most European countries of wolves attacking women and children and terrorizing whole villages during hard winters. It seems almost certain that wolves in Europe did pose a threat to human safety in some areas. However, rabies may have been the primary factor in recorded wolf attacks; most experts (Novikov 1956, Rutter and Pimlott 1968) concede that very few attacks by nonrabid animals probably occurred.

When European settlers came to the New World, they brought their fear of the wolf with them, and naturally sought to extirpate wolves whenever they were encountered. Yet, wolves in the New World apparently were different from those in the Old World, and genuine records of unprovoked attacks on humans here are very rare indeed. In fact, Mech (1970) stated that there is no acceptable evidence to support any claim that healthy wild wolves in North America are dangerous to people. The only scientifically documented case of a North American wolf attacking a man was reported by Peterson (1947): a wolf pulled a man from a railroad "speeder" and continued to attack him for about 25 minutes. Although this wolf was not tested for rabies, its extremely unusual behavior would strongly indicate that it had the disease.

There are numerous hearsay accounts of attacks by wolves, but none has ever been verified. On the contrary, there is strong evidence that the North American wolf is harmless to humans. Numerous field researchers have worked closely with the species, and none has ever reported being attacked or threatened. In fact, nearly all accounts show that North American wolves are shy animals that usually try to avoid people as much as possible.

There is no question that the wolf, wherever it occurs, can be a serious predator on domestic animals. Young (in Young and Goldman 1944) stated that there is overwhelming evidence that wolves prey upon cattle, and he listed numerous cases of such predation. He cited Joseph Neal, a stockman and conservationist from Meeker, Colorado, as stating that the history of the wolf in the West has been a chronicle of the struggle for supremacy between it and the livestock industry, with the success or failure of the livestock business depending upon the outcome. Even Theodore Roosevelt, judging from his experience on a cattle ranch in North Dakota, commented that the wolf, wherever it exists in numbers, is a veritable scourge to stockmen. Equally, it is reported that wolves played

havoc with sheep flocks. As early as 1790, wolves were serious drawbacks to sheep raising in New York (Young and Goldman 1944), and in Pennsylvania a woolen goods manufacturer failed in business because wolves destroyed his sheep in large numbers.

MANAGEMENT

History of Decline. Altogether, the role of the wolf as a predator on livestock may have been exaggerated, but it was still serious enough that settlers in North America started very early to attempt to eradicate the species on this continent. Nowak (1974) documented how these attempts to extirpate the wolf led to its decline in the Western Hemisphere. With the arrival of English settlers along the Atlantic Coast of North America, the range of the wolf began to shrink. The extreme hatred responsible for the early extermination of wolves on the British Isles was carried into the New World. By the 1880s the species had been wiped out all along the east coast of the United States, as well as in the Ohio Valley and the eastern plains. By 1914 the last wolves had been killed in Newfoundland, Canada, south of the St. Lawrence River, and in New England, New York, the Appalachians, the southern peninsula of Michigan, and much of the Great Plains region. In the following year the United States Bureau of Biological Survey began a program aimed at controlling wolf depredations on domestic stock. Partly as a result of this campaign, wolves had nearly disappeared from the western United States by 1944.

The decline in the gray wolf's range from 1944 to 1974 was much less than that of the two previous 30-year periods. The greatest recent loss seems to have occurred in Mexico, and the number of wolves moving from that country into the southwestern United States has been reduced. Otherwise, resident populations have disappeared in the Oregon Cascades, northern Wisconsin, possibly the upper peninsula of Michigan, and the Bruce Peninsula of Ontario, and on some arctic islands. Partially offsetting these losses, however, has been the reestablishment or rediscovery of wolves in certain areas, such as the Kenai Peninsula of Alaska, Glacier National Park and adjacent parts of the Rocky Mountains, and Isle Royale.

Apparently, the most critical factor in the shrinking distribution of the wolf was the spread of domestic livestock. Where cattle and sheep were raised, wolves were exterminated. Where the livestock industry was not significant, wolves were persecuted, but not to the same extent, and their numbers sometimes had a chance to rebound. The profitable limits of livestock range seem to have been reached by the 1940s, and relatively little change in the wolf's distribution has occurred since then. The one major exception is in Mexico, where wolves continue to occupy grazing lands and are under heavy human pressure. In certain other areas, such as Alberta, Ontario, and Minnesota, fairly stable lines of demarcation have existed for years between wolf range and agricultural lands. The notion that the wolf is being pushed back steadily each year does not seem altogether correct.

Within their primary range, however, wolves certainly have been intensively hunted in the last 30 years, and some populations were at least temporarily reduced. Government control programs, usually involving mass poisoning, were widespread in the 1940s and 1950s in Alaska and western Canada. Such programs were carried out mostly for the avowed purposes of protecting wild ungulates or halting the spread of rabies. Private hunting and trapping, especially from aircraft, also are thought to have reduced populations in some areas. Nonetheless, most populations seem to have remained viable, and with the general curtailment of control programs by the early 1960s, wolf numbers began to recover. Presently there is a general consensus among wildlife officials that wolves exist in safe numbers throughout most of the range they still occupy.

Current Status of the Wolf in North America. Although evaluation of numerical status would seem to be useful in determining the condition of a wolf population, such an approach presents problems. Wolves usually inhabit remote terrain, are difficult to locate, and move over great distances. There is still much to be learned about their movements, population structure, and spacing mechanisms. Estimates of numbers frequently are given, but, interestingly, those authorities most reluctant to provide estimates include some persons who have studied the wolf the longest. Even if reliable estimates were available, they would not necessarily be an effective measure of status. Numbers or population densities in a given area at a given time must be seen in a relative manner. To assess human impact on particular wolf populations, current numbers would have to be compared to those of primeval times. There is no certain way of knowing how many wolves inhabited the various regions of North America before the arrival of Caucasian mankind. Presumably, population densities approached those now found in relatively undisturbed areas where both wolves and the original kinds of prey species are fully protected. The only authority to calculate an estimate of primeval numbers was Seton (1925), who thought that the continent once had about 2 million wolves, with densities as great as 1 per 2.6 km^2, and that by 1908 about 200,000 still survived. These figures seem remarkably high in the light of present knowledge. As previously discussed, densities do not generally exceed 1 wolf per 26 km^2 even in protected areas with abundant prey, and most populations have much lower densities. One major region in which densities conceivably could have been higher is the prairie of the western United States, formerly with vast herds of bison and other large ungulates. Early travelers reported easily seeing many wolves.

Present populations densities may also be looked at relative to carrying capacity. Even if wolves exist at a lower average density than originally, they might still approach maximum levels with regard to availability of prey species. This situation may now hold in parts of northern Canada where caribou numbers are far smaller than before the introduction of firearms (see chapter 47).

Distribution, numbers, and population densities provide one idea of the status of wolf populations, and, perhaps unfortunately, most available data deal with these subjects. There are, however, other factors that must be considered in assessing the status of the wolf. The human attitudes that caused the persecution of wolves for centuries still exist to a large extent. Morever, mankind has demonstrated the technical ability to destroy wolf populations if that is desired. During the control programs of the 1940s and 1950s, poisoning and aerial gunning killed thousands of wolves in the remote tundra and taiga regions. Wolves, especially those of the far north, remain vulnerable to such activities.

Even without human dislike and direct hunting pressure, wolf populations may be under several potential threats. Economic developments now are taking place in all regions where wolves still exist. The most critical of these operations is oil and gas exploration, which is penetrating even the most remote parts of the arctic. In addition, water diversion projects, mining, and road construction are increasing in northern wilderness areas. Although such activities seldom directly affect wolves, increased human presence could mean more potential hunters and more harassment by aircraft and snowmachines. Ungulate herds, on which wolves depend, could be disrupted and their movements hindered. Some observers think that entire northern ecosystems are endangered, and, if so, then inclusive wolf populations would be threatened.

Estimates of Current Wolf Numbers. The following figures are from Nowak 1974.

Alaska: conservationists familiar with the species suggest there are between 5,000 and 10,000 wolves in the state.

Northwest Territories: 2,000 to 5,000 (Cahalane 1964).

Yukon Territory: 2,000 to 5,000 (director, Yukon Game Department).

British Columbia: 2,500 to 5,000 (Cahalane 1964).

Alberta: 3,550 in the 1965–66 period (Stelfox 1969).

Saskatchewan: 1,500 to 2,500 (Cahalane 1964).

Manitoba: 1,500 to 2,000 (government of Manitoba).

Ontario: 10,000 to 15,000 (Standfield 1970).

Quebec: 1,500 to 3,000 (Cahalane 1964).

Labrador: several hundreds (Cahalane 1964).

Michigan: upper peninsula, 6 wolves between 1971 and 1973 (Hendrickson et al. 1973); Isle Royale, "Wolf numbers continue to fluctuate above and below approximately 20 animals as they have for more than 10 years" (Mech and Rausch 1973).

Minnesota: 1,000 to 2,000 (Mech 1977).

Wyoming: Yellowstone National Park, 10 to 15 animals (Cole 1971); Shoshone National Forest, 9 in 1972; Teton National Forest, 4 in 1972.

Occasionally in recent years, wolves have been reported from or killed in Idaho, Oregon, Washington, Montana, North Dakota, South Dakota, Arizona, New Mexico, and Texas, and there may be small populations of wolves in each of these states. Else-where in the United States, wolves were extripated by the 1930s.

Mexico: no population estimates, but wolves are found in small, scattered groups in Chihuahua, Sonora, Coahuila, Durango, and Zacatecas.

Conservation Measures. Internationally, commercial traffic in wolves and wolf products is controlled by the Convention on International Trade in Endangered Species of Wild Fauna and Flora; the wolf is on appendix II of that convention. An appendix II species is one that is not necessarily threatened with extinction but that may become so unless trade is strictly regulated to avoid utilization incompatible with its survival. Permits are available for such trade where warranted.

Additionally, the wolf in the continental United States (except Alaska and Minnesota) and in Mexico is classified as an "endangered" species under the U.S. Endangered Species Act of 1973. This means that interstate trade, export, import, and take of wolves are severely regulated by the federal government. In Minnesota, the wolf has the federal classification of a "threatened" species and take and trade are also regulated, but a limited take of the species by authorized personnel is permitted in areas where wolves cause severe depredations of livestock.

In Alaska, there is no federal classification, but the wolf is classified by the state as a "big game" animal and its killing is regulated by season, limit, locality, and method. Regulations in Alaska have varied considerably over the years depending on wolf densities and other factors established by state biologists.

In Canada, the wolf is classified as "big game" in British Columbia; "predatory animal" in Northwest Territories, Yukon, and Manitoba; and "fur-bearing animal" in Alberta; it receives no classification in Saskatchewan, Ontario, and Quebec. With certain reservations, classification as "predatory animal" and "fur-bearing animal," as well as no official classification, means that wolves may be taken at any time and place, and in unlimited numbers. The "big game" classification in British Columbia allows the province to set rules and regulations governing the take of wolves.

Under the U.S. Endangered Species Act of 1973, the federal government has also determined specific areas in the lower 48 states to be "critical habitat" for the wolf. These areas are Isle Royale, Michigan, and about 26,000 km² of woodland in northeastern Minnesota. An official designation of "critical habitat" by the federal government, pursuant to the Endangered Species Act of 1973, prohibits all federal agencies from undertaking, authorizing, or financing any activities within the critical habitat area that might destroy the habitat or modify it in such a way as to prove detrimental to the survival of the species for which it is critical.

At present, the wolf is legally protected in Mexico, and cannot be taken anywhere, except under special permit issued by the federal director general of

wildlife. This regulation, however, is difficult to enforce and is not generally applied; in some areas, local stockmen apparently actively engage in efforts to eliminate the species.

THE RED WOLF

The red wolf (*Canis rufus*) is a species that has often been confused with both the gray wolf and the coyote (*Canis latrans*). In most of its range it resembles the gray wolf in color but is smaller, weighing from 18 to 34 kg, with a narrower physique and shorter fur.

The red wolf was formerly distributed from southern Pennsylvania to Florida and west to central Texas (Nowak 1979). Human persecution over the years caused a steady contraction of the species' range. Meanwhile, the more prolific coyote pushed into the range of the red wolf from the west and the north, its way opened by the elimination of the larger red wolf and environmental disruption that proved advantageous to its survival. These expanding coyote populations interbred with and eventually absorbed the scattered remnant red wolves, and by 1970 the only pure red wolves were found along the Gulf Coast of Texas and Louisiana. Eventually, even these populations succumbed to the unique process of genetic erosion, so, to the best of our knowledge, the red wolf is now extinct in the wild. About two dozen red wolves, however, were removed from the wild before the end, and were taken to breeding facilities in Tacoma, Washington. It is hoped that this small group will form a breeding nucleus that will keep the species alive and eventually provide animals for reintroductions into the wild.

Less is known about the life history of the red wolf than about that of the gray wolf or coyote. Its prey was mostly smaller than that of the gray wolf, primarily consisting of rabbits and rodents. Its home range was also smaller, about 30 km². Pairs established territories, mated in winter, and produced four or five young in the spring (Paradiso and Nowak 1972).

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