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Gray Wolf
Canis lupus and Allies

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NOMENCLATURE

COMMON NAMES. Gray wolf, timber wolf, tundra wolf, plains wolf, Spanish, lobo; French, loup; Inuktituk, amaruq; here, we use the common name "gray" wolf for the description of all subpopulations, although gray may not be the predominant color phase over large regional areas (Wilson and Reeder 1993)

SCIENTIFIC NAMES. *Canis lupus*

Subspecies. As expected in a widely distributed species, considerable variation occurs across the vast range of the gray wolf. The designation of wolf subspecies according to recently formulated criteria (e.g., Avise and Ball 1990; O'Brien and Mayr 1991), which place subspecies on a more empirical foundation, is not feasible at this time. The subspecific taxonomy of the gray wolf in North America has not been adequately analyzed by modern techniques and is unsatisfactory. A comprehensive molecular taxonomic revision of the species, using the much larger and geographically diverse collections now available, has yet to be done.

Relationships within the gray wolf are complicated by the possible introgression of genes from domestic dogs (Grace 1976; Miller 1978, 1993; Friis 1985; Wayne et al. 1992; Clutton-Brock et al. 1994) and by introgressive hybridization with coyotes (*C. latrans*) and red wolves (*C. rufus*) (Pilgrim et al. 1998; Wilson et al. 2000). Geographic variation also may have resulted from human-induced ecological disruption (Friis 1985; Lehman et al. 1991), including extirpation of local populations and their subsequent replacement by wolves of different subspecies from neighboring ranges (Nowak 1983).

Until recently, 24 subspecies of the gray wolf were recognized for North America (Hall and Kelson 1952, 1959; Hall 1981). These were based on a revision of Goldman (1944), who used cranial features, external measurements, and pelage characteristics, but did not use statistical analyses to evaluate his results. Many studies, however, cast doubt on the validity of Hall's (1981) taxonomic arrangement and suggest there are fewer subspecies (Jolicoeur 1959, 1975; Nowak 1973, 1979; Skeel and Carbyn 1977; Kolenosky and Standfield 1975; Pedersen 1982; Bogan and Mehlhop 1983; Friis 1985; Nowak 1995). Based on a cursory examination of specimens and speculation on the species's Pleistocene biogeography, Nowak (1983) suggested dividing *C. lupus* into five subspecific North American groups: northern (*occidentalis*), presumed to have originated in Beringia; southern (*nubilus*), which originated on the central plains south of the ice sheet; arctic (*arctos*), which originated in the Pearyland Refugium; eastern (*lycaon*), with origins in a southeastern refugium; and *baileyi,* a small form from the Southwest.

A more recent revision by Nowak (1995), using quantitative evaluation of cranial morphology, retained his original five subspecific designations, but revised the groupings. Mulders (1997), however, identified three subspecies of wolves in the Canadian North using statistical analyses of skull measurements. He separated mainland tundra wolves from central boreal forest wolves while retaining arctic wolves as described by Nowak (1983). In addition, new genetic analyses suggest that the eastern timber wolf (*C. lupus lycaon*) and red wolf (*C. rufus*) of the eastern United States are the same species (Wilson et al. 2000). Accordingly, the researchers proposed changing the scientific name of

both to *Canis lycaon,* with a common name of red wolf. The recommended name is based on historical precedence (Brewster and Fritts 1995). This proposal raises numerous legal, policy, and management questions.

As an alternative to conventional taxonomic classifications, Theberge (1991) proposed an ecological classification of wolf subspecies. Using major prey species and vegetation zones as the principal criteria, his classification comprises 10 categories or "ecotypes." These ecological criteria may or may not be correlated with morphological and genetic differences.

EVOLUTION

The gray wolf is a member of the Canidae, or dog family, which is part of the order Carnivora. Although a distinct taxon, it is closely related to coyotes and Simien jackals (*C. simensis*) (Wayne et al. 1995). The closest relative is the domestic dog (*C. familiaris*). Generally considered among the most morphologically primitive of the living carnivores, along with the coyote, the gray wolf is usually placed at the beginning of the systematic treatments of the order. The genus *Canis* seems to have originated from foxlike ancestors in the early to middle Pliocene (Wayne et al. 1995).

Wayne et al. (1995) suggest several wolflike species evolved from a common ancestor. *Canis lupus* first appeared in Eurasia during the Pleistocene period, about 1 million years ago. The dire wolf (*Canis dirus*) is thought to be a descendant of *Canis lupus,* which migrated to North America around 750,000 years ago. The two species seem to have coexisted for about 400,000 years. As prey began to vanish due to climate changes, the dire wolf gradually became extinct, vanishing completely about 7000 years ago.

Much recent debate has centered on the evolution and relatedness of gray wolves, red wolves, and coyotes (Wayne and Jenks 1991; Nowak and Federoff 1998; Wayne et al. 1998; Wilson et al. 2000). In theory, the wolf and the coyote are sister species, which diverged during the late Pliocene (3 million years before the present) (Nowak 1979; Wayne and O'Brien 1987). The relationship is evident from the ability of the two species to produce fertile hybrids (Kolenosky 1971). Yet, the tendency for eastern gray wolves to hybridize with coyotes is not observed in western gray wolves (Pilgrim et al. 1998; Wilson et al. 2000). In addition, red and eastern wolves share morphological characteristics not observed in western gray wolves, such as smaller size (Goldman 1944). Wilson et al. (2000) maintained that red and eastern gray wolves are more closely related to each other than either is to western gray wolves. Moreover, they believed the red wolf and eastern wolf have a common North American origin separate from that of the western gray wolf.

According to Wilson et al. (2000), North America was inhabited by a common canid ancestor 1–2 million years ago. Some of these animals traveled to Eurasia over the Bering land bridge and evolved into the gray wolf. The remaining canids evolved wholly in North America. Between 150,000 and 300,000 years ago, they diverged into the coyote, which adapted to preying on smaller mammals in the arid southwest, and the eastern/red wolf, which adapted to preying on white-tailed deer

(*Odocoileus virginianus*) in eastern forests. Gray wolves returned to the North American continent approximately 300,000 years ago, and adapted to preying on large ungulates throughout the western United States and Canada. According to this hypothesis, coyotes are more closely related to the eastern/red wolf than to the western gray wolf, therefore the propensity for interbreeding (Wilson et al. 2000).

Domestic dogs are believed to be recent derivatives of the wolf (Scott 1968; Epstein 1971; Turnbull and Reed 1974; Olsen 1985). Domesticated canids are clearly distinguishable from wolves by starch gel electrophoresis of RBC acid phosphatase (Elliot and Wong 1972). Mitochondrial DNA sequences from dogs and wolves show considerable diversity and support the hypothesis that wolves were the ancestors of dogs (Vilà and Wayne 1999). Most dog sequences belonged to a divergent monophyletic clade sharing no sequences with wolves. Contrary to earlier speculation that the domestic dog originated 10,000–15,000 years ago, the sequence divergence within this clade suggests that dogs originated more than 100,000 years before the present. Associations of dog haplotypes with other wolf lineages indicate episodes of admixture between wolves and dogs. Repeated genetic exchange between dog and wolf populations may have been an important source of variation for artificial selection. Although researchers from Israel (Mendelssohn 1982), Finland (Pulliainen 1982) and Greenland (Vibe 1981; Maargaard and Graugaard 1994) have observed matings between domestic dogs and wild wolves, none have been reported from North America. Vilà and Wayne (1999) concluded that hybridization may not be an important conservation concern even in small, endangered wolf populations near human settlements. Behavioral and physiological differences between domestic dogs and gray wolves may be sufficiently great that mating is unlikely and hybrid offspring rarely survive to reproduce in the wild.

DISTRIBUTION

The gray wolf has one of the most extensive distributional ranges of any mammal (Nowak 1983), being circumpolar throughout the northern hemisphere north of 15–20°N latitude. Except for humans the only mammalian species that has ever had a more extensive natural range is the lion (*Panthera leo*). The historical range included nearly all Eurasia and North America. Present distributions are much restricted. In recent times, the species has been extirpated from large portions of its former range and is now found mostly in remote and undeveloped areas with sparse human populations.

The gray wolf originally occupied all habitats in North America north of about 20°N latitude (Fig. 23.1). On the mainland, it was found everywhere except the southeastern United States, California west of the Sierra Nevada, and the tropical and subtropical parts of Mexico. In the southeastern United States, the red wolf replaced the gray wolf (Fig. 23.2). The species also occurred on large continental islands, such as Newfoundland, Vancouver Island, the islands off the coast of southeast Alaska, and throughout the Arctic Archipelago and Greenland, but was absent from Prince Edward Island, Anticosti, and the Queen Charlotte Islands.

An increase in the human population in North America and the expansion of agriculture initiated a general decline in the distribution and abundance of the gray wolf. At the turn of the twentieth century, wolves had nearly vanished from the eastern United States, except for some areas in the Appalachians and the northwestern part of the Great Lakes Region (Young 1944; Nowak 1983). In Canada, the species was exterminated in New Brunswick and Nova Scotia between 1870 and 1921, and in Newfoundland around 1911 (Ganong 1908; Allen and Barbour 1937; Cameron 1958; Lohr and Ballard 1996). They disappeared from the southern parts of Quebec and Ontario between 1850 and 1900 (Peterson 1966). In the prairies, the decline of the species began with the extirpation of the bison (*Bison bison*) in the 1860s and 1870s. Overhunting of other ungulate prey contributed further to the decline of gray wolves. Subsequently, in the period 1900–1930, intensive predator control aimed at the eradication of wolves virtually eliminated the species from the western United States and adjoining parts of Canada. By 1960,
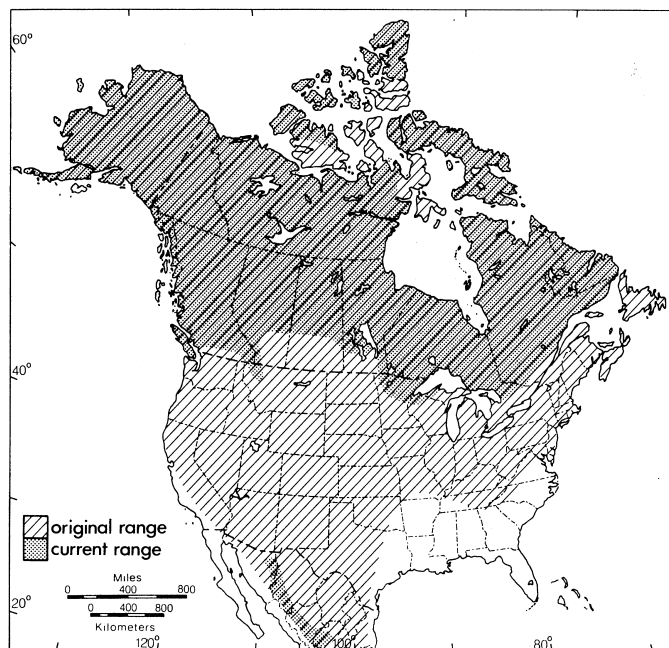

FIGURE 23.1. Past and present distribution of the gray wolf (*Canis lupus*).

the wolf was exterminated by federal and state governments from all of the United States except Alaska and northern Minnesota.

In the 1930s to the early 1950s, the decline in distribution and abundance was reversed, particularly in southwestern Canada (Nowak 1983). This recovery was the result of expanding ungulate populations—following improved regulation of big game hunting—and a moderation in predator control programs (Gunson 1995). The increase in the number of wolves triggered the resumption of wolf control in western and northern Canada, which resulted in the killing of thousands of wolves from the early 1950s to the early 1960s, mostly by poisoning (Heard 1983; Stardom 1983; Hayes and Gunson 1995). Recovery followed the cessation of indiscriminate control and by the mid-1970s wolf populations had increased.

The distribution of the gray wolf in North America is now confined primarily to the northern half the continent (i.e., Alaska and Canada). In the conterminous United States, populations exist in northern Minnesota, northern Wisconsin and Michigan's Upper Peninsula, and parts of Washington, Idaho, and Montana. A program to reintroduce wolves from Alberta and northeastern British Columbia to Yellowstone National Park and Idaho was carried out in 1995 and 1996, respectively. In the Southwest and Mexico, the Mexican wolf (*C. l. baileyi*) is effectively extinct in the wild, but a small number survives in captivity. Reintroductions were begun in Arizona and New Mexico in 1998.

In Canada, the gray wolf is still found throughout most of its historical range including coastal islands (Miller and Reintjes 1995 (Paquet and Darimont 2002). The species is completely gone from insular Newfoundland, Nova Scotia, and New Brunswick and is absent or rare in the densely populated and developed parts of the other provinces. Overall distribution of the species in Canada has not changed substantially in the last 40 years and still constitutes approximately 80% of the historical range (Carbyn 1983a). In many areas within its world wide range, wolf populations have been decimated or completely extirpated, which makes Canada an important stronghold of the species.

DESCRIPTION

The gray wolf is the largest living canid. Externally, the gray wolf resembles a large domestic dog, such as a husky, but usually differs in having proportionally longer legs, larger feet, and a narrower chest (Banfield 1974). The wolf's face can be distinguished by its wide tufts of hair, which project down and outward from below the ears (Mech
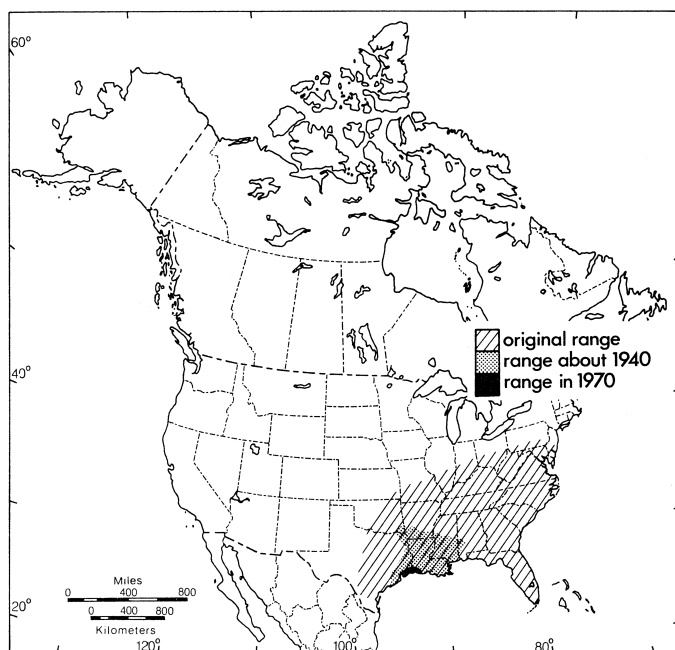
FIGURE 23.2. History of the distribution of the red wolf (*Canis rufus*).

1970). A wolf's tail is straight and does not curl up posteriorly as with some domestic dogs. Adult wolves, except melanistic individuals, have white fur around the mouth, but dogs usually have black fur in this area.

Mature males weigh from 20 to 80 kg, depending on subspecies, and vary in total length from 1.27 to 1.64 m. Shoulder height varies from 66 to 81 cm. Adult females are usually smaller, weighing from 16 to 55 kg, and are 1.37 to 1.52 m in total length (Young and Goldman 1944; Mech 1970, 1974). The overall size and weight of wolves increase from southern to northern latitudes. For more discussion on weight in *C. lupus,* see Mech (1970, 1974) and Young and Goldman (1944).

Wolves are digitigrade, walking so only the toes contact the ground. The front foot has five toes; the first is rudimentary and does not reach the ground, but has a well-developed dew claw. The hind foot has four toes. The claws are not retractable, are blunt, and are nearly straight. Depending on weight, adult wolves have a foot load of 89–114 g/cm^2 (Formozov 1946; Nasimovich 1955). 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 most dogs, tracks of wolves are more elongated, have the front two toe prints closer together, and show the marks of the front two toenails more prominently.

The red wolf resembles the gray wolf in most respects but is smaller in average size. Total length is usually about 1300–1600 mm and weight usually 20–35 kg for males and 16–25 kg for females. The red wolf has longer legs, larger ears, and shorter fur. The color is not really red, as in a red fox (*Vulpes vulpes*), but much like that of most *C. lupus,* with a stronger reddish tinge to the flanks and limbs. Some gray wolves, however, also are reddish, especially on the west coast of British Columbia and Alaska. A dark-colored or black phase of *C. rufus* apparently was locally common in the heavily forested parts of the range of the species.

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

Coloration of wolves is highly variable and usually of little use in ascertaining the geographic origin of specimens, although arctic populations are predominantly white. Over most of the range, "gray" wolves vary from a pure white to coal black. The usual color is 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. Dark or all-black wolves are more common in the interior of western Canada and Alaska than the conterminous United States. Standfield (1970) stated that, in Ontario, wolves to the north of Lake Superior varied in pelage color from white to black, but those 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 tactile organs. A group of stiff hairs surrounds the precaudal gland on the back about 70 mm above the base of the tail. These hairs are usually tipped with black, even in animals that are otherwise 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. The largest skulls of *C. lupus* on record (one was 305 mm in greatest length) are from 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 (Fig. 23.3). A skull of *C. familiaris* of equivalent size can usually be distinguished by a much more massive, steeply rising frontal region (a usual result of which is a higher orbital angle; see Mech 1970) and its relatively smaller teeth.

Teeth of wolves are designed to tear and cut large chunks of meat and to crush and crack bone. The normal dental formula for all members of the genus *Canis* is I 3/3, C 1/1, P 4/4, M 2/3. 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 first lower molar form the carnassials. Molars of wolves retain a flattened or chewing surface, but not to the same extent as in the coyote, which depends more on vegetable matter in its diet.

GENETICS

The karyotype of the wolf appears to be the same as that of the domestic dog (diploid number $2n = 78$). The autosomal complement is 38 acrocentric chromosomes in decreasing order of size. The X is the largest submetacentric chromosome and Y the smallest meta- or submetacentric. Thus, the fundamental number (n.f. after Stains 1975) is 80 (Chiarelli 1975). Since the early 1970s (Seal et al. 1975), many molecular studies have been carried out to resolve taxonomic and conservation problems related to *Canis lupus* and other canids (Kennedy et al. 1991; Lehman et al. 1991, 1992; Wayne et al. 1991, 1992; Roy et al. 1994, 1996; Meier et al. 1995; Forbes and Boyd 1996, 1997; García-Moreno et al. 1996; Vilà and Wayne 1999).

The pattern of genetic diversity in sexually reproducing species is principally due to genetic drift, gene flow, and natural selection (Allendorf 1983). Of these three factors, genetic drift is probably not important with respect to the pattern of variation observed in the gray wolf, as it would be if it occurred in small, isolated populations. The second factor, gene flow, is related to the dispersal of reproductive individuals among demes. Because the wolf is a highly vagile species, considerable gene flow is expected among demes (Forbes and Boyd 1996). This would help maintain genetic similarity among demes. Distance alone, however, may act to reduce gene flow (Chesser 1983). Whereas gene flow tends to reduce variation among populations, differential directional natural selection tends to act in the opposite direction and maintain divergence among demes. Gene flow and natural selection are probably the principal factors underlying the observed within-species diversity in wolves.

An alternative view (Shields 1983) holds that, without disruptions, philopatry would limit dispersal and promote breeding within packs, thus maintaining variation among demes. Studies of the genetic relationships of wild populations (Kennedy et al. 1991; Lehman et al. 1992; Wilson et al. 2000) suggest that significant outbreeding takes

relationship. Their results suggest that the DNA of the eastern Canadian wolf and the red wolf is not of gray wolf origin, but is similar to that of coyotes because of their recent divergence from a common ancestor (see Evolution).

PHYSIOLOGY

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 generally is not a direct threat to the survival of individuals.

REPRODUCTION AND DEVELOPMENT

Mech (1974) summarized the breeding data on wolves, and much of the following is based on his discussion. A more comprehensive review is provided by Asa and Valdespino (1998). The wolf has a high reproductive potential, although the rate of reproduction may be adjusted to the carrying capacity of the environment (Mech 1970). Wolves mate from January to April, depending on latitude. Courtship takes place between pack members or between lone wolves that pair during mating season. The female is in estrus for 5–7 days and blood may flow from the vulva for a few days to a few weeks before estrus (Carbyn 1987). Not all females in a wolf pack produce pups (Harrington et al. 1982). The dominant pair within a pack usually breeds, with subdominant females under behaviorally induced reproductive suppression (Packard et al. 1985). Subordinates occasionally reproduce successfully (Paquet et al. 1982; Harrington et al. 1982; Van Ballenberghe 1983b; Packard 1985). Reproduction of female wolves may be regulated by aggression among females, direct interference during copulation attempts, or deferred reproduction by younger females (Packard et al. 1983; Asa et al. 1990). Copulation is in typical canine fashion, with the bulbous base of the male's penis locking into the female's vaginal sphincter, the tie lasting up to 30 min.

The young are born in spring after a gestation period of 62–63 days. Birth dates extend from early April to early June. Birth usually occurs in a sheltered place in a hole, rock crevice, hollow log, or overturned stump. Duration of lactation is 8–10 weeks. Litter size averages 6 and ranges from 1 to 11. Young are blind and deaf at birth and weigh an average of 450 g. They become sexually mature between 9 and 46 months (Lentfer and Sanders 1973; Medjo and Mech 1976), but generally do not mate until they are at least 3 years old because of the social structure of the pack. Average age of sexual maturity is 22 months. Longevity is up to 13 years in the wild (Mech 1988) and 16 years in captivity. Mech (1975) found, by examining wolf litters, that males were more common in high-density populations. Kuyt (1972) also found male pups were predominant in the Northwest Territories.

A pack generally has one to three breeding females, but other adults in the pack help in rearing the young. Behavioral limitations on mating, including mate preferences, may hold the productivity of wolves considerably below the theoretical maximum, and often only one litter of pups is born, even in large packs. The instinct to raise the young appears strong among most pack members. Two lone-female wolves and a lone-male wolf each successfully raised litters of young in northwestern Montana and southeastern British Columbia. This unusual reproductive behavior occurred in a low-density population of wolves colonizing an area containing a relatively dense population of ungulates (Boyd and Jimenez 1994). A surrogate female adopted four orphaned pups in Banff National Park. She successfully reared the litter and was able to lactate, although never pregnant (P. Paquet, unpublished data).

In an unexploited population, an estimated 60% of adult females breed, compared with 90% in populations exploited by humans (Rausch 1967). The ability of wolves to respond to increased mortality is also reflected by the percentages of pups in unexploited versus exploited populations. In Wood Buffalo National Park, the percentage of pups in a population under natural control escalated from 20% to 35% one year
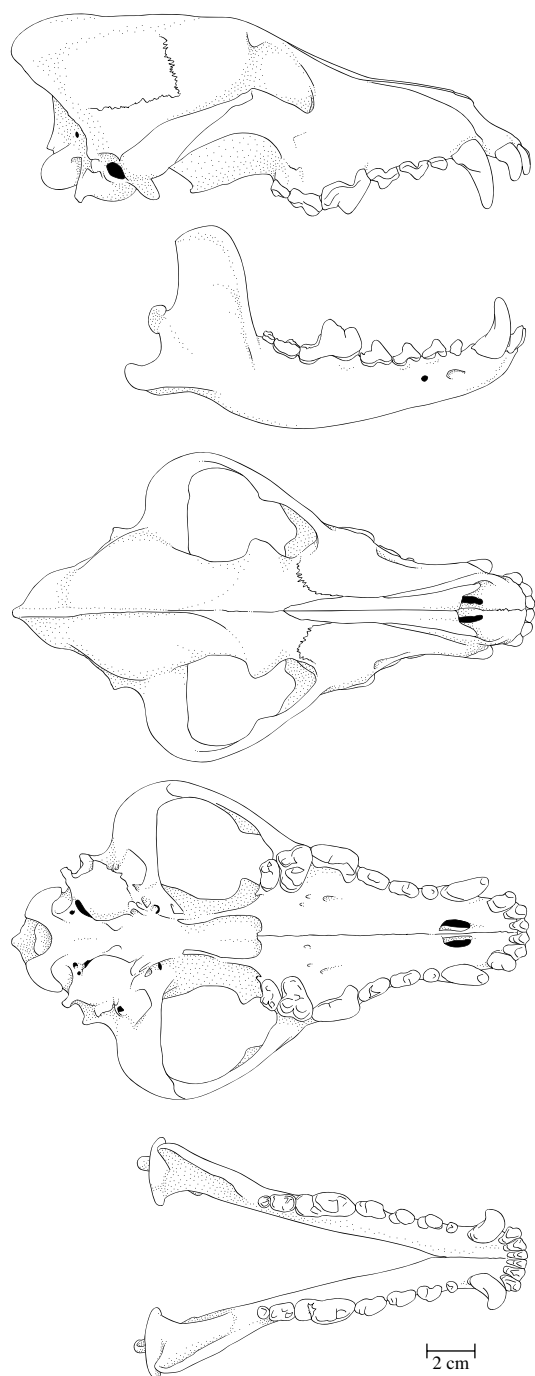

FIGURE 23.3. Skull of the gray wolf (*Canis lupus*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

2 cm

place. Little regional genetic differentiation may occur (Wayne et al. 1992). Hybridization appears to occur 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).

Lehman et al. (1991) suggested coyote genes have introgressed into sympatric North American gray wolf populations. One explanation of this relationship was that "hybridizing wolves" contained similar amounts of coyote genetic material to the red wolf (Roy et al. 1994). The similarity between the eastern wolf and the red wolf has been noted previously. Both species were described as small eastern wolves long before the eastward expansion of coyotes occurred (Brewster and Fritts 1995). Recent studies by Wilson et al. (2000) may have clarified the

after wolf control was initiated and to 55% two years later (Fuller and Novakowski 1955). Similar results were obtained in the Great Slave Lake area. There, wolf control resulted in an increased percentage of pups, 46% and 73% one and five years later, compared with 13% under natural control (Kelsall 1968). Studies in Alaska (Rausch 1967) showed no decline in an exploited population where the pup–adult ratio remained at around 44:56. On the other hand, the wolf population in the Great Slave Lake area, with a pup–adult ratio of 73:27, was declining. Mech (1970) concluded from these findings that wolves can compensate, by increased reproduction, for annual losses of at least 50% of animals 5 months or older. We believe this figure is high if recruitment through immigration is not included. Our calculations suggest that 30–40% would be more realistic, whereas Keith (1983) established a value of about 30% of the fall population.

The 36% reproductive success is the lowest on record. Reproductive success from other studies has ranged between 62% and 93% (Messier 1985b; Potvin 1987). Ideally, it is necessary to measure the percent of pups in a fall or winter population (annual recruitment) because this reflects both natality and survival of juveniles through the summer relative to adults (Peterson 1977; Fritts and Mech 1981).

Development of Pups. Hillis and Mallory (1996a), working in the Northwest Territories, examined 73 fetuses from 16 wolves. Fetuses grew at a mean rate of 5.17 g/day between day 32 after coitus and parturition. During the same period, fetuses increased in length at a mean rate of 0.204 cm/day. No significant sexual dimorphism in body mass or other morphological features was found at this stage of development. Hillis and Mallory (1996b) also compared 22 skeletal, visceral, and adipose characteristics of 425 adult wolves. Fifteen parameters differed significantly by sex. Males were usually larger than females. The degree of sexual dimorphism, however, varied with structure. The authors concluded that sexual dimorphism in wolves has evolved primarily as a foraging strategy, owing to division of labor between the sexes, and males are more highly specialized for capturing and killing large ungulate prey; females are more specialized for a nurtural role.

As with other altricial mammals, wolves are born helpless. Neonates are blind and deaf, have little ability to thermoregulate, and receive assistance from the mother to eliminate wastes (Mech 1970). Van Ballenberghe and Mech (1975), working in northern Minnesota, obtained weights, growth rates, canine tooth lengths, and survival data from 73 wild wolf pups. Relative weights of wild pups were expressed as percentages of a standard weight curve based on data from captive pups of similar age. These relative weights varied greatly within litters, among litters, and among years; extremes of 31–144% of the standard were observed. Growth rates ranged from 0.05 to 0.23 kg/day, and similar variations in general development and in replacement and growth of canine teeth were noted. Survival data based on radio-tracking and tag returns indicated that pups with relative weights <65% of standard had a poor chance of survival, whereas pups of at least 80% of standard weight had high survival.

Home Sites, Dens, and Rendezvous. Wolf home sites are important and comparatively small areas where reproductive activities take place. Pups are born, fed, raised, and protected in the natal and secondary den sites, a series of rendezvous sites, and surrounding areas. Research on wolf dens has been conducted in Alaska (Rausch 1969; Stephenson 1974; Chapman 1977; Ballard and Dau 1983; Lawhead 1983), Canada (Criddle 1947; Mech and Packard 1990; Coscia 1993; Bloch in Paquet 1993), and Minnesota (Fuller 1989; Ciucci and Mech 1992). In other studies, wolf den characteristics and den-site selection have been topics peripheral to the main objectives of research (Murie 1944; Haber 1968, 1977 [Alaska]; Joslin 1966, 1967 [Ontario]; Banfield 1954 and Clark 1971; Walton 2000 [Canadian Arctic]; and Carbyn 1975a [Canadian Rockies]). Several studies have investigated habitat features associated with den-site selection and construction (Joslin 1966; Clark 1971; Carbyn 1975a; Stephenson 1974; Ryon 1977; Ballard and Dau 1983; Ciucci and Mech 1992; Heard and Williams 1992; Matteson 1992; Walton 2000). For example, investigators have identified secondary

dens, and dens are sometimes found at rendezvous sites (Haber 1968; Clark 1971; Chapman 1977).

A den is an underground burrow or other sheltered place used by wolves (Young and Goldman 1944; Banfield 1954; Lawhead 1983). Wolves visit and prepare one to several den sites within their home range as much as 4–5 weeks before giving birth (Jordan et al. 1967; Haber 1968; Clark 1971; Stephenson and Johnson 1973). As parturition nears, the pregnant female remains near the selected den (Young and Goldman 1944; Mech 1970). Wolf dens may be burrow systems, hollow logs, spaces between roots of trees, caves or crevices in rocks, abandoned beaver (*Castor canadensis*) lodges, or expanded mammal burrows. Pups also have been born in excavations in snow (Kelsall 1960), on surface beds at the base of spruce trees (Soper 1942), and in very shallow surface dens (Mech 1970). Most dens face south or near south; their exposure to sun and wind is such that the den area is often snow free at the onset of denning (Clark 1971; Stephenson 1974). Banfield (1954), however, noted one den where the burrow length included 1 m of snow. Generally, dens are near a source of water (Joslin 1967; Haber 1968; Clark 1971; Voigt 1973; Stephenson 1974; Carbyn 1975a). Rendezvous sites are characteristically centered near open, grassy areas bordered by trees or thickets with water within 50 m of the site (Joslin 1967; Pimlott et al. 1969; Van Ballenberghe et al. 1975).

The natal den serves a brief but important purpose by providing protection from the elements and potential predators for the first few weeks of life. Temperature and humidity in the den are generally moderate and stable compared with the outside environment. Even after pups emerge from the den and begin to eat semisolid food regurgitated by adults, at 3–4 weeks (Mech 1970), wolf dens temporarily remain the center of activity, the point from which adults go out to hunt and to which they return with food for the young.

Dens may be found at locations other than where pups are born. Multiple den sites within a given pack's home range may be concentrated in a small area. For example, five dens were found within a 15-km^2 area in Jasper National Park (Carbyn 1975a). Two or more dens may be within a few hundred meters of each other, with other dens several kilometers away (Banfield 1954; Clark 1971). In Mount McKinley National Park, pairs of dens were approximately 0.2, 0.3, and 0.4 km apart (Chapman 1977). In those few reported cases where single packs had two litters of pups, the dens were 6.4 km (Murie 1944) and 3.2 km (Clark 1971) apart. Average distance between dens of neighboring packs in Alaska was 45 km (Ballard et al. 1987). Denning areas of three neighboring packs occupying islands in coastal British Columbia were separated by <500 m of water (C. Darimont, University of Victoria, Victoria, British Columbia, pers. commun., 2001).

Rendezvous sites are areas where pups are left, usually with an adult, while pack members forage. Rest and play dominate the activities at rendezvous sites (Theberge 1969). They are characteristically centered near open, grassy areas that are bordered by trees or thickets with sources of water within 50 m (Joslin 1967; Pimlott et al. 1969; Van Ballenberghe et al. 1975). In coastal areas, estuaries provide ideal habitat for coastal rendezvous sites (Darimont and Paquet In press). Abandonment of rendezvous sites appears to occur during September or October at all latitudes (Pimlott et al. 1969; Clark 1971; Voigt 1973; Van Ballenberghe et al. 1975). In coastal British Columbia, rendezvous sites near salmon streams often are used until runs are exhausted in late October and beyond (C. Darimont and P. Paquet, pers. obs.).

Repeated use of established natal dens and rendezvous sites has occurred in as many as 15 consecutive years (P. Paquet, pers. obs.). Several authors report natal den and rendezvous sites being used 4 consecutive years (Clark 1971; Voigt 1973; Peterson 1974; Carbyn 1975a). In Minnesota, den use was traditional in 86% of the denning alpha females studied for >1 year (Ciucci and Mech 1992). Voigt (1973) found that one rendezvous site was used at least five times, and four others at least three times, during a period of 9 years. Rendezvous sites may be occupied several times within the same year (Pimlott et al. 1969, P. Paquet, pers. obs.).

Availability of stable sources of food and water, suitable physical characteristics for den construction, location of neighboring packs, and

security from human activity may influence den location. As discussed in Van Ballenberghe and Mech (1975:59), "The quality and quantity of prey eaten and the frequency of its composition probably influence the growth of wild wolf pups more than any other single factor." Thus, to the extent that the den's location helps, or impedes, swift, easy access to prey, placement of the den plays a role in the health of the pups until the time of its abandonment. Den selection in the arctic and subarctic was related to prey availability (Chapman 1977) and habitat characteristics (Heard and Williams 1992; Walton 2000). Within the tree-line zone of the taiga, wolves preferred to den where the roots of trees and shrubs provided structural support for their tunnels (Heard and Williams 1992). The denning area of a wolf pack in Jasper National Park was near elk (*Cervus elaphus*) calving grounds and several mineral licks (Carbyn 1975b). Kuyt (1972) and Clark (1971) noted that migratory wolves often move to denning areas before caribou (*Rangifer tarandus*) begin to migrate through. They also found that wolves usually denned along the major caribou migration routes. Heard and Williams (1992) reported that most wolves on migratory caribou ranges in the Northwest Territories denned near the northern limit of tree growth. The density of dens in the forest was lower than expected if dens were randomly dispersed. Within the tundra zone, wolves did not show any preference for denning near caribou calving grounds.

Wolves in northern Montana used dens that were the greatest distance possible from human disturbance (D. Boyd, University of Montana, Missoula, pers. common., 1992). Wolf dens within the central 60% of winter territories in northeastern Minnesota were randomly located compared with territory centers (Ciucci and Mech 1992). Only 10.5% of the dens were within a 1-km-wide strip inside the territory boundaries, suggesting possible avoidance of neighboring packs. A negative relationship between territory size and den distance from territory centers also was found, suggesting that in large territories wolves might select the denning site that reduces travel distance from and to the den. Lack of suitable denning sites can be a limiting factor in poorly drained tundra (Fleck and Gunn 1982).

Pups are usually born during the first 2 weeks of May in Mount McKinley National Park (Haber 1968). In the Arctic, most pups are whelped between mid-May and early June (Kelsall 1968; Clark 1971; Stephenson 1974), during late April to early May in southeast Alaska (Garceau 1960), early to mid-April in Wood Buffalo National Park (Soper 1942), early to mid-May in Algonquin Provincial Park (Rutter and Pimlott 1968), mid-April to mid-May in Jasper National Park (Carbyn 1975a), and mid-March to late April in Isle Royale National Park and in Minnesota (Van Ballenberghe and Mech 1975).

The age at which pups are carried or led from the natal den to another den or rendezvous site varies considerably. Joslin (1966) reported that one pack moved its litter to a new den when the pups were <3 weeks old. The usual time for pups to leave the natal den seems closer to that reported by Murie (1944), who observed packs abandoning natal dens when the pups were 8–10 weeks old. In Mount McKinley National Park, most recorded dates for the movement of pups to a secondary den or a rendezvous site were between early June and early July, when pups are 4–8 weeks old (Haber 1968). In 1976, however, a natal den was used until approximately 24 August (Matteson 1992). Arctic wolves usually leave natal dens in July, but moves have been reported in early June and in August (Stephenson and Johnson 1972). On Baffin Island, abandonment of natal dens occurred between early July and early August, when pups were 4–9 weeks old (Clark 1971). In southern Canada and in Minnesota, it is probably unusual for pups to remain at natal dens beyond 1 July (Mech 1970). In Jasper National Park, pups were moved between late May and mid-June, when they were 3–6 weeks old (Carbyn 1975a). In Alaska, natal dens were usually abandoned between late June and late July (Ballard et al. 1987). Earlier abandonment resulted from human disturbance.

Reported movements of pups from natal dens to secondary dens averaged 3 km and ranged from 0.3 to 11.2 km (Chapman 1977). Duration of occupancy of secondary home sites is quite variable and has ranged from 2 to 90 days. Termination of rendezvous site use apparently occurs during September or October at all latitudes (Pimlott et al.

1969; Clark 1971; Voigt 1973; Peterson 1974; Van Ballenberghe et al. 1975).

ECOLOGY

Habitat Use. The gray wolf once occurred in all major habitats including deserts, grasslands, forests, and arctic tundra. Because wolves are not highly habitat specific, move long distances, and require large home ranges, the species is regarded as a habitat generalist (Mech 1970; Fuller et al. 1992; Mladenoff et al. 1995). Populations, however, are adapted to local conditions and specialized concerning den-site use, foraging habitats, physiography, and prey selection (Fritts et al. 1995; Mladenoff et al. 1995, 1997, 1999; Paquet et al. 1996; Alexander et al. 1996, 1997; Haight et al. 1998; Mladenoff and Sickley 1998; Callaghan 2002). Thus, wolves are better characterized as ecosystem generalists that are idiosyncratic concerning the surroundings in which they live. Habitat use by wolves is strongly influenced by availability and abundance of prey (Carbyn 1974, 1975a; Keith 1983; Fuller 1989; Huggard 1991, 1993a; Weaver 1994; Paquet et al. 1996), snow conditions (Nelson and Mech 1986a, 1986b; Fuller 1991a, 1991b; Paquet et al. 1996), protected and public lands (Woodroffe 2000), absence or low occurrence of livestock (Bangs and Fritts 1996), road density (Thiel 1985; Jensen et al. 1986; Mech 1988; Fuller 1989; Thurber et al. 1994; Mladenoff et al. 1995, 1997, 1999; Alexander et al. 1996), human presence (Mladenoff et al. 1995; Paquet et al. 1996; Callaghan 2002), and topography (Paquet et al. 1996; Callaghan 2002). Although wolves continue to occupy diverse regions of North America, the species is no longer present in areas with dense human populations or those under intense cultivation (Mladenoff et al. 1995, 1997; Paquet et al. 1996; Mladenoff and Sickley 1998; Haight et al. 1998; Callaghan 2002). Protected and public lands likely encourage wolf presence because of fewer lethal encounters with humans (Mech 1995). Due to conflicts with ranchers, wolves are prone to local extirpation in areas with high densities of livestock (Bangs and Fritts 1996; Bangs et al. 1998, 2001).

Home Range. Many researchers have reported that packs of wolves occupy stable home ranges that are exclusive territories (Mech 1970, 1974; Peterson et al. 1984; Messier 1985a, 1985b). Territorial behavior is thought to be a spacing mechanism, which adjusts wolf densities to their food level. In some circumstances, however, home ranges are dynamic and nonexclusive. Reasons for this instability are not well understood, but likely relate to availability of food. Forshner (2000) reported home ranges of wolves in Ontario overlapped extensively. Others found the areal extent and geographic location of home ranges changed among years (Carbyn 1981, 1982b; Potvin 1987; Mech et al. 1995a).

Biologists usually define the home range of a wolf as an area within which it can meet all of its annual biological requirements. Seasonal feeding habitat, thermal and security needs, travel, denning, and the bearing and raising of young, are all essential life requirements. The manner in which habitats are used and distributed influences home range size and local and regional population distributions. Generally, wolves locate their home ranges in areas where adequate prey are available and human disturbance minimal (Mladenoff et al. 1995, 1997; Mladenoff and Sickley 1998) and seem to cognitively map their territories (Peters 1978, 1979). Wolves use areas within those home ranges in ways that maximize encounters with prey (Huggard 1993a, 1993b). In mountainous areas, selection of home ranges and travel routes is influenced by topographic complexity (Paquet et al. 1996). Wolf use of valley bottoms and lower slopes corresponds to the presence of wintering ungulate prey and snow depth in these areas (Singer 1979; Jenkins and Wright 1988; Paquet et al. 1996). In areas of higher prey density, pack sizes increase (Messier 1985b) and home range size is closely correlated with pack size (Peterson et al. 1984; Messier 1985b). Mech (1970) and Ballard et al. (1997) suggested that wolves denning on the tundra and relying on migratory caribou range over larger areas than wolves occupying forested areas and relying on resident prey.

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The size of a pack's home range varies considerably from area to area, depending principally on the type and density of prey and season. Territory and home range sizes are more closely correlated with pack size than with prey density (Peterson et al. 1984; Messier 1985b). In areas of higher prey density, pack sizes increase. Messier (1985b) concluded that between 0.2 and 0.4 moose/km^2, the territory area per wolf is independent of moose abundance. A colonizing pack might have a larger, more fluid home range than a pack surrounded by other wolf packs (Boyd et al. 1995; Boyd and Pletscher 1999). Territories tend to be smaller in summer, when packs are tied to dens and home sites (Mech 1977a). No such restrictions exist in winter, which allows wolves to roam more freely. In Algonquin Park, where the principal prey is deer, territories ranged from 104 to 311 km^2 (Pimlott et al. 1969). In the boreal areas, sizes of home ranges reported and the predominant prey are as follows: 283 km^2 (deer, *Odocoileus virginianus;* moose, *Alces alces;* elk) in central Manitoba (Carbyn 1981); 568 km^2 (195–629 km^2 in summer, 357–1779 km^2 in winter) (moose) in northern Alberta (Fuller and Keith 1980); and 1250 km^2 (bison) in Wood Buffalo National Park (Oosenbrug and Carbyn 1982). In the mountain zone, home ranges in the Rocky Mountains range from 1058 to 3374 km^2 (Paquet 1993) and in the Yukon from 583 to 794 km^2 (Hayes et al. 1991). In the arctic region, home ranges on Ellesmere Island were >2500 km^2 (Mech 1987, 1988). Winter-territory size in Minnesota averaged 78–153 km^2 (Fuller 1989).

Population Densities. Keith (1983) and Fuller (1989) reviewed numerous studies of North American wolf populations and concluded that average wolf densities are correlated with the biomass of ungulates available per wolf. Densities of wolves are highest where prey biomass is highest (Keith 1983; Fuller 1989; Fuller and Murray 1998). In North America, reported wolf densities range from 1/2 km^2 to 1/3274 km^2 for stable populations (Table 23.1) Average annual wolf densities do not often exceed about 1 wolf /24 km^2 and are usually far lower. Pimlott (1967) suggested that 1 wolf/20–25 km^2 was the maximum density tolerable by a natural wolf society. During certain periods of exceptionally high prey concentrations, however, the density of wolves may increase dramatically (Mech 1974). For example, Kuyt (1972) reported that in some parts of the Northwest Territories (Mackenzie), winter wolf densities can be compressed to 1 wolf/10 km^2 as a response to high concentrations of migrating caribou. In 1998, at least 633 wolves were killed in an area of about 8000 km^2 in the Rennie Lake region of the Northwest Territories, or about 1 wolf /13 km^2 (D. Cluff, Government of Northwest Territories, Yellowknife, Northwest Territories, pers. commun., 2001). Van Ballenberghe et al. (1975), working in Superior National Forest, found a 550-km^2 area in which the density of wolves reached an average of about 1/14 km^2.

The highest density of wolves ever recorded was 1/2 km^2 at a winter deer yard near Algonquin, Ontario (Forbes and Theberge 1995), reflecting a seasonal concentration of wolf packs. Wolves reintroduced to Coronation Island, Alaska, reached a density of about 1/8 km^2 before dying out (Merriam 1964; Klein 1995). Sustained densities of about 1 wolf/13–29 km^2 have been reported on coastal islands of Alaska (Person 2001) and British Columbia (Darimont and Paquet 2000). The lowest reported density is 1 wolf /3274 km^2, on Ellesmere Island in the Canadian Arctic. In the central Canadian Rocky Mountains, density was 1 wolf /250–333 km^2 over 10 years (Paquet et al. 1996; Callaghan 2002). This is the lowest reported density in North America for a stable population. The lowest reported density in forested, nonmountainous regions is 1 wolf /260–500 km^2 in Ontario (Pimlott et al. 1969).

Movements. Movement patterns of gray wolves have been studied in much of their current range in North America (Fritts and Mech 1981, Messier 1985a, 1985b; Potvin 1988; Ballard et al. 1997). Most studies were of territorial wolves that prey on ungulates including deer, elk, moose, and sheep (*Ovis* spp.). Although some of these ungulates may undergo seasonal migrations, they are of lesser magnitude than the migrations of barren-ground caribou (*Rangifer tarandus groenlandicus*). Consequently, most studies have concluded that wolves maintain relatively stable annual territories. Migratory wolves, however, have

TABLE 23.1. Winter density for various North American wolf populations within broadly defined regions

Region	Density (wolf/km2)	Reference
Great Lakes/St. Lawrence		
Quebec	1/20–50	Banville 1983
	1/50–100	
	1/100–1000	
Ontario Algonquin Park	1/26	Pimlott et al. 1969
	1/2	Forbes and Theberge 1995
Ontario	1/60–130	Kolenosky 1983
Ontario Pukaskwa N.P.	1/104–139	P. Paquet, pers. obs.
Michigan Isle Royale N.P.	1/20–25	Jordan et al. 1967
	1/11–33	Peterson and Page 1988
Boreal		
Quebec	1/50–100	Banville 1983
	1/100–1000	
	1/71–125	Messier 1985b
Ontario	1/130–260	Kolenosky 1983
Minnesota	1/32	Mech 1973
	1/24	Van Ballenberghe et al. 1975
	1/17–35	Fuller 1989
Manitoba wolf range	1/500	R. Stardom, pers. commun.
Riding Mountain N.P.	1/30–109	P. Paquet, pers. obs.
Prince Albert N.P.	1/74–85	Parks Canada, pers. commun.
Alberta wolf range	1/55–78	J. Gunson, pers. commun.
Alberta Oil Sands	1/128	J. Gunson, pers. commun.
Swan Hills	1/90	Fuller and Keith 1980
Fort McMurray	1/158	Fuller and Keith 1980
Wood Buffalo N.P.	1/89	Oosenbrug and Carbyn 1982
	1/83	Gunson 1995
Simonette River	1/40–66	Gunson 1995
Nordegg	1/42	Gunson 1995
Mountain		
Alberta, Jasper N.P.	1/250–333	Gunson 1995
	1/111–143	
	1/250–500	
Alberta, Banff N.P.	1/250–333	Paquet et al. 1996
British Columbia	1/70–171	Tompa 1983
	1/100–110	Bergerud and Elliot 1986
Arizona	1/109	Theberge 1991
Pacific		
Vancouver Island	1/12–17	Tompa 1983
Arctic		
Barren Grounds	1/154–307	Kelsall 1957
	1/588	Kelsall 1968
	1/500	Parker 1972
	1/11–13	Parker 1973
Baffin Island	1/255	Miller 1993
Southern tier of islands	1/329	Miller 1993
Queen Elizabeth Islands	1/2026	Miller 1993
Ellesmere Island	1/3274	Miller 1993
	1/900	Riewe 1975
Alaska	1/71	Boertje et al. 1996
Alaska Kenai	1/50–91	Peterson et al. 1984
Alaska south central	1/97–385	Ballard et al. 1987
	1/227–667	Ballard et al. 1997

been documented in wolf–caribou systems in northern Canada and Alaska (Parker 1973; Stephenson and James 1982; Ballard et al. 1997; Walton 2000; Walton et al. 2001) and wolf–bison ecosystems in Wood Buffalo National Park, Northwest Territories (Carbyn et al. 1993).

Movements by wolves can be divided into migrational movements following prey, movements within territories, and dispersal (Mech 1974). Travel patterns of wolves are influenced by elevation, topography, distribution of important prey, and seasonal changes of climate. Wolves prefer the easiest possible traveling and therefore make use of logging roads, survey lines, trails, lake shores, and passes between hills. Although wolves appear to select areas of low road density (see below), travel routes are generally close to trails and roads (Gehring 1995; Singleton 1995; Boyd-Heger 1997; Callaghan 2002). Ski

trails, snowmobile trails, ploughed roads, and snow-packed roads can enhance the range and efficiency of winter forays (Singleton 1995; Paquet et al. 1996). Highways, other human structures, and human activities may impede or alter use of travel routes (Paquet and Callaghan 1996; Paquet et al. 1996; Boyd-Heger 1997). Elevation can also govern seasonal movements of wolves. In mountainous areas with high snowfall, use of low-elevation valleys increases during winter, where frozen rivers and lakes, shorelines, and ridges are preferred because of ease of travel. Singleton (1995) suggested that variation in pack size, variation in home range size, and interactions with sympatric predators may also influence habitat use and travel patterns. Musiani et al. (1998) reported an average travel speed of 3.78 km/hr for wolves in Bialowieza Primeval Forest, Poland. Wolves moved faster on forest trails, roads, and frozen rivers than in the forest. In addition, individuals traveling with other pack members moved faster than those walking alone. On Ellesmere Island, Northwest Territories, mean travel speed of wolves was measured during summer on barren ground at 8.7 km/hr during regular travel and 10.0 km/hr when returning to a den (Mech 1994b).

Daily distances traveled in a pack's territory can range from a few kilometers up to 200 km (Mech 1970). On Isle Royale, a pack of 16 wolves travelled 443 kilometers over 31 days, an average of 14.3 km/day (Mech 1966). In Alaska, Burkholder (1959) followed a pack that averaged 24 km/day for 15 days. Mech (1970) reported daily movements of 1.6–4.6 km for wolves preying on deer. Kolenosky (1972) found that a pack of eight wolves in Ontario traveled 327 km over 46 days, averaging 7.1 km/day. Peterson (1977) calculated the average daily distance traveled by packs on Isle Royal between 1971 and 1974 was 11.1 km. Oosenbrug and Carbyn (1982) reported daily movements of 2.3–18.7 km for wolves preying on bison. Five wolves traveled about 32 km along the coast of northeastern Bathurst Island in about 5 hr (F. Miller, Canadian Wildlife Service, Edmonton, Alberta, pers. commun., 1999).

Migration. Migration involves the seasonal movement of a pack between widely separated geographic locations. Migratory wolf populations are those that depend on caribou, especially migratory barrenground caribou, but also woodland caribou. Movements of migratory wolves are generally long term, involve entire packs, and can be related to the availability of preferred food on the resident territory. Both Stephenson and James (1982) and Ballard et al. (1997) suggested that migration of wolves following caribou is not always an annual event. If wolves have sufficient access to prey on resident territories, migration probably represents a historical pattern that has evolved. When prey such as caribou are highly aggregated and predictable, strict territoriality may be abandoned and the social system swings toward "group" nomadism.

In the western Arctic of Alaska, wolf packs usually did not follow migratory caribou, but maintained year-round resident territories, which averaged 1868 km^2 (Ballard et al. 1997). Wolves only migrated with the western Arctic caribou herd in years when alternate ungulate prey densities were too low to sustain wolf packs (Ballard et al. 1997). Pack areas and territories did not normally overlap, but when overlaps occurred, packs were separated temporally. Wolves in south-central Alaska did not follow migratory movements of moose or caribou (*Rangifer tarandus granti*) outside their pack areas, but did follow elevational movements of moose within their areas (Ballard et al. 1987). Differing migratory strategies of Alaskan wolves may be related to the availability of moose as an alternative prey (Stephenson and James 1982; Ballard et al. 1997).

Radio-collared wolves in the Northwest Territories and western Nunavut showed a distinct migratory pattern associated with movements of caribou. Packs left tundra denning areas in autumn and moved over large areas throughout the winter before returning to the tundra to give birth in early spring. Returning wolves began to restrict movements around den sites on the tundra by late April. Thus, they did not exhibit territorial behavior typical of other wolf populations in North America (Walton et al. 2001). Annual home range sizes averaged 63,058 km^2 for males and 44,936 km^2 for females. Home range in summer

averaged 2022 km^2 for males and 1130 km^2 for females. Straight-line distances from the most-distant location on the winter range to the den site averaged 508 and 265 km, respectively.

Dispersal. Dispersal involves the movement of an individual away from the territory of its birth and its pack. Dispersal movements are important for gene flow among demes and aid in the establishment of new packs. Wolves may increase their reproductive fitness by dispersing as yearlings, but remaining in packs as older adults. Dispersal in wolves appears as a gradual and dynamic dissociation process. As offspring begin to mature, they disperse from the pack as young as 9 months of age (Fritts and Mech 1981; Messier 1985a; Fuller 1989; Gese and Mech 1991). Separation from the pack may extend from a few months to several years (Messier 1985a). Most wolves disperse when 1–2 years old, and few remain with the pack beyond 3 years of age (Mech et al. 1998). Thus, young members constitute a temporary portion of most packs and the only long-term members are the breeding pair (Mech 1999b).

Dispersal may be directional long-distance travel or nomadic (Carbyn 1987; Boyd and Pletscher 1999). Some evidence suggests that wolf packs colonize areas that were first "pioneered" by dispersing lone wolves (Ream et al. 1991; Pletscher et al. 1991, 1997). Dispersing wolves are often deposed alpha animals or younger, low-ranking pack members (Zimen 1975, 1976) driven away by aggression over food or mates. In the Yukon, dispersal rate was density independent and related to mean pack size and prey biomass–wolf index (Hayes and Harestad 2000a). Yearling and pup dispersal rates in Minnesota were highest when the wolf population was increasing or decreasing and low when the population was stable (Gese and Mech 1991). Potvin (1987) concluded dispersal in Quebec resulted from the onset of sexual maturity and, possibly, from social stress. A study in Minnesota recorded up to six exploratory moves were made before dispersal (Fuller 1989). Conversely, Boyd and Pletscher (1999) found most dispersing wolves left their natal home range quickly after separating from the pack.

Wolves that disperse frequently try to establish new packs. Most new packs are likely formed by dispersers (Rothman and Mech 1979; Fritts and Mech 1981; Fuller 1989; Boyd and Pletscher 1999). Pack fission is another mechanism (Mech 1966; Meier et al. 1995). Dispersing wolves typically establish territories or join packs within 50–100 km of their natal pack (Fritts and Mech 1981; Fuller 1989; Gese and Mech 1991; Boyd et al. 1995; Wydeven et al. 1995). Some wolves, however, move longer distances. Some reported dispersal distances are 206 km in 2 months (Mech 1974), 670 km in 81 days (Van Camp and Gluckie 1979), and 20–390 km for five dispersing wolves (Fritts and Mech 1981). In Alaska, several wolves from the same pack traveled 732 km in a 9-month period (Ballard et al. 1983). Fuller (1989) reported that dispersing wolves traveled 5–100 km during periods of 1–265 days. Dispersing wolves in Quebec traveled an average distance of 40 km (Potvin 1987). Fritts (1983) reported a record dispersal distance for a male wolf of 886 km. A yearling female dispersed a record 840 km from the Rocky Mountains in Montana north into British Columbia (Boyd et al. 1995).

Wolves may disperse at any age but young wolves do so more frequently. In north Minnesota, most dispersers left when they were 11–12 months old, and only a few wolves dispersed as adults (Gese and Mech 1991). In Papineau–Labelle Reserve, most wolves dispersed when they were 10–20 months old (Potvin 1987). Several studies found both sexes disperse equally (Fuller 1989; Gese and Mech 1991; Boyd et al. 1995; Boyd and Pletscher 1999). In Alaska, however, 74% of dispersers were males (Ballard et al. 1987). Rates of dispersal appear to vary with age and environmental conditions. Annual dispersal rates in northern Minnesota were about 17% for adults, 49% for yearlings, and 10% for pups (Fuller 1989). Of 316 wolves monitored in Superior National Forest, Minnesota, 75 were dispersers. Eight percent of adults, 75% of yearlings, and 16% of pups dispersed (Gese and Mech 1991). In Alaska, 28% of 135 wolves dispersed from their original area (Ballard et al. 1987).

The times of reported dispersals vary, although January–February seems consistent among studies. In north-central Minnesota, pups left

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natal packs during January–March and older wolves left frequently during September–April (Fuller 1989). Dispersal occurred mainly in February–April and October–November in another Minnesota study (Gese and Mech 1991). Dispersal in Alaska occurred mainly during April–June and October–November (Ballard et al. 1987). January–February and May–June were peak periods for wolf dispersal in the northern Rockies (Boyd and Pletscher 1999).

The fate of dispersing wolves is probably related to their age, the density of a wolf population, availability of prey, availability of unoccupied habitat, and presence of humans (Fuller 1989; Gese and Mech 1991; Boyd et al. 1995). In northern Minnesota, adults dispersed short distances into nearby territories, but yearlings and pups dispersed short or long distances. Adults had the highest pairing and denning success, yearlings had a moderate pairing and low denning success, and pups had low pairing and denning success. Yearlings and pups that dispersed a short distance had a higher success of settling in a new territory, which likely reflected available vacancies in nearby territories (Gese and Mech 1991). (Fuller 1989) found only 1 disperser joined an established pack, but 16 others formed new packs. In Alaska, 28% of 135 wolves dispersed from their original area. Twenty-two were accepted into existing packs (Ballard et al. 1987). Dispersers in a newly established population produced more litters than biders (philopatric wolves) (Boyd and Pletscher 1999). Annual survival rate for dispersers and biders did not differ. Proportionately more dispersers (90%) than biders (60%) died of human causes.

Interactions with Other Carnivores. As summit predators, gray wolves likely have a profound influence on other top carnivores (Hairston et al. 1960). However, except for coyotes (Fuller and Keith 1981; Carbyn 1982b; Schmitz and Kolenosky 1985a, 1985b; Meleshko 1986; Paquet 1991a, 1991b; 1992; Thurber et al. 1992; Peterson 1995; Arjo and Pletscher 1999) and red foxes (Peterson 1995), competition between wolves and other carnivores has been the focus of relatively few studies. Interference competition is the best-known mechanism by which wolves subordinate other carnivores (Ballard 1982; Gehring 1993) or are themselves displaced (Ballard 1982; Hornbeck and Horejsi 1986). Interference occurs when competitively subordinate species are aggressively displaced, killed, driven away, or choose to avoid more dominant wolves. Resource competition and exploitation competition, which are indirect and difficult to demonstrate, have not been documented.

Wolves can exclude coyotes from individual pack territories to entire regions. However, coexistence also is common (Paquet 1991a, 1991b, 1992; Thurber et al. 1992) and the outcome of competition may be influenced in subtle ways by topography, snow cover, seasons, food abundance, niche overlap, population characteristics, and the overriding influence of humans (Peterson 1995). In theory, wolves might affect other predators by reducing availability of ungulates, or conversely, by increasing availability of carrion. Less obvious influences of wolves might include modified community relationships. By providing carcasses for scavenging, wolves might affect interactions of sympatric canids, ursids, felids, mustelids, and avian scavengers such as ravens (*Corvus* spp.) and bald eagles (*Haliaeetus leucocephalus*). Ravens, for example, appear to fly toward howling, especially in winter when wolves are killing large animals and carrion may be available (Harrington 1978). Wolves might affect brown bears (*Ursus arctos*) by reducing the availability of a limiting resource (possibly an ungulate) or, conversely, by increasing the carrion available to bears (Ballard 1982). In complex systems with multiple prey and predators, all of these relationships would become increasingly more complicated.

Fatal encounters have been documented between wolves and cougars (*Puma concolor*) (Schmidt and Gunson 1985; White and Boyd 1989; Boyd and Neale 1992), wolves and coyotes (Seton 1925; Young and Goldman 1944; Munro 1947; Stenlund 1955; Berg and Chesness 1978; Carbyn 1982a; Fuller and Keith 1981; Paquet 1991b), wolves and red foxes (Stenlund 1955; Mech 1970; Banfield 1974; Allen 1979; Peterson 1995), wolves and black bears (*U. americanus*) (Rogers and Mech 1981; Ramsay and Sterling 1984; Horejsi et al. 1984; Paquet

and Carbyn 1986), wolves and grizzly bears (P. Paquet, unpublished data), wolves and polar bears (*U. maritimus*) (Ramsay and Sterling 1984), wolves and wolverines (*Gulo gulo*) (Burkholder 1962), and wolves and river otters (*Lontra canadensis*) (Route and Peterson 1991; Kohira and Rexstad 1995). Depredation is not necessarily motivated by food attainment, as carcasses of wolf-killed carnivores are often not consumed (Carbyn 1982a; Paquet 1991b). Characteristically, smaller canids (Wobeser 1992) and cougars (White and Boyd 1989) killed by wolf aggression are not eaten, but left with fatal bites in the head and neck and frequent puncture wounds through the torso.

FEEDING HABITS

Wolves are obligate carnivores whose use of prey depends largely on the availability and vulnerability of ungulates (Weaver 1994). Beavers, hares (*Lepus americanus*), other smaller mammals, and scavenging (Forbes and Theberge 1992) supplement the diet, particularly during wolf denning and rendezvous site activities. In North America, important ungulate prey include deer (see citations throughout chapter), moose (Atwell 1964; Frenzel 1974; Peterson 1977; Bergerud et al. 1983; Messier 1984; Potvin et al. 1988; Forbes and Theberge 1996b; Ballard and Van Ballenberghe 1997), caribou (Banfield 1954; Kuyt 1972; Bergerud 1974; Seip 1992; Dale et al. 1994; 1995; Adams et al. 1995; Boertje et al. 1996; Ballard et al. 1997), elk (Cowan 1947; Carbyn 1983b; Paquet 1992; Huggard 1993b, 1993c; Larter et al. 1994; Kunkel et al. 1999), bison (Oosenbrug and Carbyn 1982; Carbyn and Trottier 1987, 1988; Joly and Messier 2000; Smith et al. 2000), muskoxen (*Ovibos moschatus*) (Gray 1970, 1983; Heard 1992; Mech 1999a), mountain goats (*Oreamnos americanus*) (Smith 1983; Fox and Streveler 1986; Festa-Bianchet et al. 1994), and mountain sheep (Murie 1944; Haber 1977; Gasaway et al. 1983; Hoefs et al. 1986; Paquet et al. 1996). When two or more ungulate species inhabit the same area, wolves usually concentrate on the smallest or easiest to catch (Mech 1970; Paquet 1992; Weaver 1994; Paquet et al. 1996). Most ungulate prey are young, weakened, debilitated, or older animals (Fuller and Keith 1980; Carbyn 1983b; Paquet 1992), although wolves do kill healthy adult animals. The proportion of debilitated prey may be higher than reported, as wolves are keen observers of behavior, able to detect subtle susceptibilities not evident to humans (Frenzel 1974).

Stephenson and James (1982) reported that caribou constituted 97% and 96% of the biomass consumed by two radiocollared wolf packs during winter. Calves constituted 20% and 6% of caribou killed by the same two packs during summer. In the Nelchina Basin of south-central Alaska, 72% of 330 kills located during winter were moose. Fox and Streveler (1986) found that 62% of wolf scats in the northern coast ranges of southeastern Alaska contained mountain goat remains. Kuyt (1972) found caribou were the staple diet of wolves on caribou winter ranges. Fuller (1962), working in Wood Buffalo National Park, recorded bison remains in 39 of 95 stomachs of poisoned wolves. Oosenbrug and Carbyn (1982) and Joly and Messier (2000), also working in Wood Buffalo National Park, confirmed that bison were the primary prey for wolves. The major prey of two packs of Vancouver Island wolves were black-tailed deer (*Odocoileus hemionous*), elk, and beaver, respectively. In the southern Rocky Mountains of Canada and northern Rockies of the United States, elk were the most common prey species (Cowan 1947; Huggard 1993b; Boyd et al. 1994; Weaver 1994; Paquet et al. 1996; Kunkel et al. 1999), followed by deer and mountain sheep. Moose predominated in the diet of wolves in north-central Alberta (Fuller and Keith 1980). Elk, moose, and white-tailed deer were the major prey species in Riding Mountain National Park (Carbyn 1983b). In the Superior National Forest of northeastern Minnesota, white-tailed deer constituted 80% of dietary occurrences during winters of 1946–1948 (Stenlund 1955) and 56% and 66% of summer and winter occurrences, respectively, in scats during 1969–1971 (Van Ballenberghe et al. 1975). In north-central Minnesota, deer were the primary prey in winter and spring, but beavers were an important secondary prey (20–47% of items in scats) during April–May. Neonatal deer fawns occurred in 25–60% of scats during June–July, whereas the

occurrence of beavers declined markedly. Overall, deer provided 79–98% of biomass consumed each month. Adult wolves consumed an estimated 19 deer/year, of which 11 were fawns (Fuller 1989).

Packs have increased energetic demands when raising pups (Mech 1970). Those demands can be met seasonally by higher rates of kill, more complete use of carcasses, and increased consumption of small mammals such as beavers (Meleshko 1986; Potvin et al. 1992a). Nevertheless, most studies of the summer diet of gray wolves show ungulates are the predominant source of biomass consumed. Use of fawns and calves increases, apparently related to availability and not local abundance (Murie 1944; Cowan 1947; Mech 1966; Pimlott et al. 1969; Clark 1971; Kuyt 1972; Carbyn 1975a; Van Ballenberghe et al. 1975; Voigt et al. 1976; Peterson 1977; Scott and Shackleton 1980; Peterson et al. 1984; Messier and Crète 1985; Meleshko 1986; Ballard et al. 1987; Potvin et al. 1988; Fuller 1989; Thurber and Peterson 1993). In the Nelchina Basin of south-central Alaska, analysis of wolf scats collected at den and rendezvous sites indicated moose represented 53% and caribou 7% of the summer diet by occurrence (Van Ballenberghe 1991). Kuyt (1972) found caribou constituted 47% of food items during spring and summer in mainland Northwest Territories. The type and quantity of food consumed by wolves while attending den and rendezvous sites is of interest to researchers. Theberge et al. (1978), and Scott and Shackleton (1980) found scat collected on trails and at rendezvous sites differed significantly in content. Carbyn (1983b) reported that wolf scats collected along trails were the same in content as those collected at rendezvous sites. Fuller and Keith (1980) also reported similar results.

Beavers, lagomorphs, microtine rodents, and a variety of birds (especially waterfowl) (Kuyt et al. 1981) and their eggs supplement the diet of wolves. Fish, berries, and carrion are consumed seasonally where available (Young and Goldman 1944; Bromley 1973; Meleshko 1986; Kohira and Rexstad 1995; Darimont and Paquet 2000). Coastal wolves also feed on marine mammal carcasses, crabs, mussels, and even barnacles (Darimont and Paquet 2000). Wolves occasionally scavenge at refuse dumps, rubbish bins, and bone yards even when wild prey are available (Fuller and Keith 1980; Krizan 1997). On occasion, wolves kill and consume other carnivores such as bears (Rogers and Mech 1981; Ballard 1982; Ramsay and Stirling 1984; Horejsi et al. 1984; Paquet and Carbyn 1986) and river otters (Route and Peterson 1991; Kohira and Rexstad 1995; Paquet pers. obs.). These minor food items may be sustaining between periods of ungulte kills, during declines in ungulate populations, or while wolves are denning and using rendezvous sites. For example, wolves denning in the Canadian Arctic may subsist on small mammals, birds, and fish when their primary prey, caribou, migrate to summer range (Kuyt 1972; Williams and Heard 1993; Williams 1995). Tener (1954), working on Ellesmere Island, recorded remains of arctic hare (*Lepus arcticus*) in 83% of 70 summer and winter scats.

Peterson (1977) reported beaver remains in 76% of the scats collected on Isle Royale. Voigt et al. (1976), in central Ontario, found beavers represented 55–75% of occurrences in summer scats. Frequent occurrence of beavers throughout the year has been reported for Vancouver Island (Scott and Shackleton 1980; Milne et al. 1989) and southeastern Alaska (Kohira and Rexstad 1995). Milne et al. (1989) attributed this year-round use to the mild winter of the region. Although beavers are common food items in some regions of North America, they do not control the distribution or abundance of wolves (National Research Council 1997).

As mentioned above, wolves occasionally consume fish. Francis (1960) reported six wolves feeding on concentrations of minnows and water bugs in a hole in the frozen Torch River, Saskatchewan. Young and Goldman (1944) record instances of wolves catching spawning salmon (*Oncorhyncus* spp.). A wolf pack on midcoast British Columbia was documented catching and partially consuming >200 salmon during one night (C. Darimont, University of Victoria, British Columbia, pers. commun., 2001). Adult wolves in the same pack were observed catching >20 salmon/hr. Often, wolves consume only the head, leaving the rest for a diversity of scavengers (Paquet pers. obs.). Wolves in areas of low ungulate densities use more alternative foods, especially during summer

(Voigt et al. 1976; Peterson 1977; Messier and Crète 1985; Ballard et al. 1987). On Isle Royale, the incidence of beaver in scats increased from 13–15% to 76% during a time of high beaver populations and low moose productivity. Seasonal declines in ungulate density occur in areas where caribou migrate to calving grounds in early spring. Thus, many wolf packs that prey on caribou during winter become separated from caribou during summer (Kuyt 1972; Williams and Heard 1993; Williams 1995; Walton et al. 2001). Banfield (1954) suggested that small, nonungulate prey might be critically important in the summer diet of wolves denning in areas where caribou are migratory. Pimlott (1967) believed that wolves would prey on low numbers of caribou when other ungulate prey were not available. Subsequent studies have supported his argument that caribou or other ungulates are the primary source of food for wolves in summer and winter (Clark 1971; Kuyt 1972; James 1983; Meleshko 1986; Ballard et al. 1987; Dale et al. 1994; Spaulding et al. 1998). Dale et al. (1994) found no evidence of prey switching owing to changes in ungulate abundance. Wolves continued to prey on caribou even when moose were twice as abundant. Spaulding et al. (1998) reported that wolves switched to preying on moose during winter in years when caribou numbers were low and moose were more vulnerable because of snow conditions, but by June of each year caribou were again the predominant prey item. Wolves in the Yukon did not show a strong switching response away from moose as the ratio of caribou to moose increased in winter (Hayes et al. 2000).

Kill and Consumption Rates. The reported rates of kill and food consumption by wolves vary considerably. Hebblewhite (2000) concluded the wide array of methods used to estimate kill rates confounds attempts to compare studies. Much of the variation likely reflects the remarkable ability of wolves to adjust to seasonal and annual availability, vulnerability, distribution, and abundance of ungulate prey. Regional differences in size and energy requirements of wolves might also explain some differences in rates of predation (Oosenbrug and Carbyn 1982). For example, wolves in Wood Buffalo National Park are substantially larger than wolves in eastern North America. In the early 1970s, Isle Royale wolves exhibited an immediate response to high moose vulnerability by increasing their kill rate. As kill rate went up, wolf use of carcasses declined. During these years, killing another moose was easier for wolves than digging out frozen remains of an old carcass (Peterson and Allen 1974). Throughout most North America, the condition of winter snow, particularly the interaction of depth and hardness, could be an important determinant of prey susceptibility and rates of predation (Kolenosky 1972; Peterson and Allen 1974; Haber 1977; Peterson 1977; Carbyn 1983b). Kill rates often increase as the depth of snow increases (Peterson and Allen 1974; Mech and Nelson 1986; Huggard 1993a, 1993b; Paquet et al. 1996; DelGuidice 1998). Fuller (1991a) reported wolves in north-central Minnesota changed winter activity, movement patterns, sociality, and feeding behavior in response to snow-induced changes in deer distribution and mobility.

Surplus or excessive killing by wolves of caribou (Miller et al. 1985) and white-tailed deer (DelGuidice 1998) has been reported. In Minnesota, excessive killing by wolves related to poor physical condition of deer owing to effects of a severe winter. The authors predicted excessive killing will occur when snow depth exceeds 70 cm for 4–8 weeks. In the Northwest Territories, Miller et al. (1985) found 34 newborn caribou calves killed by wolves. The calves were killed within minutes of each other and clumped in a 3-km^2 area. Wolves did not feed on 17 of the carcasses and only partially ate the other 17. Miller et al. (1985) reported that a single wolf killed three calves on one occasion and three and four calves on a second occasion at average kill rates of 1 calf/min, 1 calf/8 min, and 1 calf/6 min, respectively, between first and last deaths. They attributed surplus killing of newborn caribou calves to their high densities and vulnerability on calving grounds.

A pack of five wolves in Riding Mountain National Park, Manitoba, under extreme late winter conditions killed at the rate of 1 elk, white-tailed deer, or moose every 2.7 days (Carbyn 1983b). Fuller and Keith (1980) found a summer kill rate of 1 moose every 4.7 days for a pack of 10 wolves in Alberta. The mid- to late winter predation

rate of wolves in Wood Buffalo National Park was 1 bison/7.8 days (Oosenbrug and Carbyn 1982). In Alaska, wolf predation rates during summer were 1 kill/7–16 days, whereas winter rates were 1 kill/5–11 days. Large packs killed ungulates more frequently than did smaller packs. Kill rates per wolf, however, were greater for smaller packs (Ballard et al. 1987). Kill rates by wolves on a rapidly growing moose population in the east-central Yukon reached 2.4 moose/wolf/100 days (Hayes and Harestad 2000a). Kill rates by individual wolves were inversely related to pack size and unrelated to prey density or snow depth (Hayes et al. 2000). In Banff National Park, where seven species of ungulate prey are sympatric with wolves, the predation rate of wolf packs averaged 1 kill/3 days. This was composed of 1 elk/4.4 days, 1 mule deer/25 days, 1 white-tailed deer/46 days, 1 bighorn sheep/59 days, and 1 moose/67 days (Hebblewhite 2000).

Most estimates of food consumption by wolves (summarized by Mech 1970 and Schmidt and Mech 1997) are made by calculating the weight of edible material available from a carcass and dividing that by the number of wolves and days. The method, however, does not account for underuse of carcasses by wolves (Peterson 1977; Paquet 1992), food lost to scavengers (Carbyn 1983b; Messier and Crète 1985; Ballard et al. 1987; Fuller 1989; Hayes et al. 1991; Paquet 1992; Thurber and Peterson 1993; Dale et al. 1995), and undetected caching (Murie 1944; Cowan 1947; Mech 1988; Mech et al. 1998; Mech and Adams 1999). In Riding Mountain National Park, 91% of wolf-killed elk and 86% of wolf-killed moose were abandoned before all edible portions had been consumed. Large wolf packs consumed a higher proportion than small wolf packs (Paquet 1992). Promenberger (1992) found that large groups of juvenile ravens removed up to 37 kg of food/day from fresh ungulate carcasses. He suggested these flocks were more important competitors with small than large wolf packs because fewer wolves consume kills more slowly than larger packs. Hayes et al. (2000), studying a recovering wolf population in the Yukon, confirmed that scavenging by ravens decreased the amount of prey biomass available for wolves to consume, especially for wolves in smaller packs.

As noted above, wolves can adjust to a wide variation in amount of food available, and will eat as much as four times their daily their maintenance requirement of 1.7 kg/wolf (Mech 1970). A mean daily rate of >3.2 kg/wolf is required for successful reproduction (Mech 1977a). On Isle Royale, Mech (1966) estimated daily consumption of moose at 4.4–6.3 kg/wolf. Peterson (1977), also working on Isle Royale, calculated daily winter food consumption of 6.21–10.0 kg/wolf during 1971–1973 and 4.4–5.0 kg/wolf during 1974. In Ontario, Pimlott et al. (1969) and Kolenosky (1972) estimated a daily rate of consumption of 3.8 and 2.9 kg/wolf, composed primarily of white-tailed deer. Mech and Frenzel (1971) calculated a daily rate of consumption in northeastern Minnesota of 2.7 kg/wolf. Daily winter consumption averaged 2.0 kg deer/wolf in north-central Minnesota (Fuller 1989). In Riding Mountain National Park, wolves consumed about 8 kg of prey/day under unusual winter conditions and high elk densities (Carbyn 1983b). Daily per capita consumption of wolves in northeastern Alberta varied between 0.12 and 0.15 kg prey/kg wolf (Fuller and Keith 1980). The daily consumption of bison in Wood Buffalo National Park was 5.3 kg/wolf. A pack of eight wolves rearing five pups required 2526 kg of edible meat between 1 May and 1 October (Fuller and Keith 1980).

Predator–Prey Relations. Wolves specialize on vulnerable individuals of large prey (e.g., elk and moose), yet readily generalize to common prey such as deer and beavers. As a species, wolves display remarkable behavioral plasticity in using different prey and habitats (Mech 1991; Weaver et al. 1996). Although wolf predation has been investigated in more than 35 locales (Fuller 1989; Gasaway et al. 1992; Messier 1994), most studies have involved one or two ungulate species. Potvin et al. (1992b) studied the effects of wolf predation on beaver in Papineau–Labelle Reserve, Queebec. Studies of wolf predation amid high ungulate diversity are limited (Cowan 1947; Carbyn 1974, 1975a, 1983b; Paquet 1992; Huggard 1993a, 1993b, 1993c; Boyd et al. 1994; Kunkel et al. 1999; Hebblewhite 2000). This is due, in part, to wolf extirpation where multiple prey species are common (Young and Goldman 1944).

Keith (1983) and Fuller (1989) found ungulate biomass per wolf is highest for heavily exploited (Ballard et al. 1987) or newly protected (Fritts and Mech 1981) wolf populations and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982; Mech 1986) or those where ungulates are heavily harvested (Kolenosky 1972). Wolf densities lower than predicted by Keith (1983) and Fuller (1989) were charcterized by high ungulate diversity in which at least one prey species occurred in large groups (Weaver 1994). Crète and Manseau (1996) compared the biomass of ungulates with primary productivity along a 1000-km latitudinal gradient on the Québec–Labrador peninsula, and Crète (1999) did the same over North America. For the same latitude, ungulate biomass was five to seven times higher in areas where wolves were absent than where wolves were present. In areas of former wolf range, but where no wolves currently exist, a regression of ungulate biomass to primary productivity produced a positive slope (Crète 1999). Thus, elimination of wolves from an area adapted to an evolutionary history of strong predator–prey interactions may have a severe impact through a trophic cascade (Terborgh et al. 1999).

Interactions of ungulates and their predators may overshadow habitat capability as a controlling factor for ungulate populations. Many researchers have reported wolf predation decreases survival and population growth rates of ungulate populations (Gauthier and Theberge 1986; Gasaway et al. 1992; Potvin et al. 1992a; Hatter and Janz 1994; Boertje et al. 1996; Jedrzejewska et al. 1997; Bergerud and Elliot 1998; Kunkel and Pletscher 1999; Hayes and Harestad 2000a). Despite difficulties in applying rigorous experimental design to wolf–prey studies (Boutin 1992; Orians et al. 1997; Minta et al. 1999), many researchers have concluded that wolf predation can limit, and possibly regulate, populations of moose, caribou, and white-tailed deer (Bergerud et al. 1983; Messier and Crète 1985; Gauthier and Theberge 1986; Messier 1991, 1994, 1995b; Skogland 1991; Gasaway et al. 1992; Seip 1992, Van Ballenberghe and Ballard 1994; Boertje et al. 1996; Ballard et al. 1997; Eberhardt 1997; Messier and Joly 2000; Hayes and Harestad 2000a; Hayes et al. 2000; but see Boutin 1992; Theberge 1990; Theberge and Gauthier 1985; Thompson and Peterson 1988). Potvin et al. (1988) suggested that under certain conditions, wolf predation can have antiregulatory effects on white-tailed deer.

Group size, landscape structure, and winter severity may influence whether wolf predation is density dependent or density independent. The functional and numerical responses of wolves to changing prey density likely vary with prey species, availability of alternative prey, presence of other predators (Messier 1994; Eberhardt 1997; Eberhardt and Peterson 1999), habitat overlap, herd sizes, and herd behavior (Huggard 1993b, 1993c; Weaver 1994; Hebblewhite 2000). In diverse prey systems, wolf predation may shift among species depending on annual fluctuations in winter severity (Nelson and Mech 1986a; Paquet 1992; Huggard 1993a; Post et al. 1999) or landscape changes (Weaver et al. 1996). Where wolf predation is a factor, ungulates may exist at levels well below carrying capacity for relatively long periods. Unusually mild or severe winter weather can result in ungulate populations that are temporarily higher or lower than predicted habitat potential (which reflects long-term average maximum). Wolf packs may react to changing conditions in varying ways, depending on the location of their territories in relation to other packs and prey distribution (Nelson and Mech 1986b; Mech 1994a). If packs have lower prey densities within their territories, they may exploit territories more intensely. This may be achieved by (1) persevering in each attack, (2) using carcasses thoroughly, (3) feeding on alternative and possibly second-choice food resources such as beaver (Messier and Crète 1985), and (4) patrolling their territory more intensely (Messier 1985b).

Messier (1984, 1991, 1994, 1995b) and Messier and Crète (1985) proposed that two-state equilibrium models best described the dynamics of wolf predation on ungulates. Eberhardt (1998) and Eberhardt and Peterson (1999), however, concluded that single-state models were adequate. In multiprey systems, the stability, or equilibrium, of ungulate prey and wolf populations seems to depend on a variety of factors, including wolf predation rate, number and age of ungulates killed by hunters, ratio of ungulates to wolves, and population growth rate of

different ungulate species (Cowan 1947; Carbyn 1983b; Huggard 1991; Weaver 1994; Kunkel and Pletscher 1999). Elk are the primary prey of wolves in many multiple-prey systems, and are often the preferred prey when available (Carbyn 1983b; Paquet 1992; Huggard 1993b; Weaver 1994; but see Kunkel et al. 1999). The consequences of wolf preference for elk on population dynamics are complex due to prey switching (Oaten and Murdoch 1975), alternate prey increasing predator density at low primary prey density (Messier 1994, 1995☐), spatial distribution of multiple prey species (Iwasa et al. 1981), and differential encounter rates across species (Messier 1994, 1995b).

Most studies emphasize the direct effects (e.g., prey mortaliy) wolves have on the population dynamics of their ungulate prey (Carbyn 1975a; Mech and Karns 1977; Carbyn 1983b; Gasaway et al. 1983; Gunson 1983; Peterson et al. 1984; Messier and Crète 1985; Ballard et al. 1987; Boutin 1992; Messier 1994; Hayes and Harestad 2000a). However, predation can also profoundly affect the behavior of prey, including use of habitat, time of activity, foraging mode, diet, mating systems, and life histories (Sih et al. 1985). Accordingly, several studies describe the influence wolves have on movements, distribution, and habitat selection of caribou moose, and white-tailed deer (Carbyn 1975b; Mech 1977c; Rogers et al. 1980; Nelson and Mech 1981; Bergerud et al. 1984; Stephens and Peterson 1984; Messier and Barrette 1985; Ballard et al. 1987; Messier 1994). A failed wolf attack on barren-ground caribou changed the movement pattern of a postcalving herd. Three attacking wolves caused the caribou to reverse their direction of travel, recross a river, and return to the direction from which they had come (Scotter 1995). Wolves can increase the rate at which they accrue resources by seeking out areas with dense concentrations of prey (Huggard 1991; Weaver 1994; Hebblewhite 2000). Prey, in turn, can lower their expected mortality rate by preferentially residing in areas with few or no wolves. Several studies have suggested that ungulate prey seek out predator-free refugia to avoid predation by wolves (Mech 1977c; Holt 1987; Paquet 1993; Hebblewhite 2000). Wolf predation in the Superior National Forest of northern Minnesota affected deer distributions within wolf territories (Mech 1977c). Densities were greater along edges of territories where predation was thought to be less. Nelson and Mech (2000), however, observed female white-tailed deer remained on their traditional home ranges despite proximity to wolf home sites and did not attempt to reduce exposure to wolves by moving away.

Recent evidence suggests the importance of cascading trophic interactions on terrestrial ecosystem function and processes (Glanz 1982; Emmons 1984; Terborgh 1988; Terborgh et al. 1999). Accordingly, system-wide effects of wolf predation may be more profound than previously expected. For example, on Isle Royale, Michigan, wolf predation on moose positively influenced biomass production in trees of boreal forest (McLaren and Peterson 1994). Growth rates of balsam fir (*Abies balsamea*) were regulated by moose density, which in turn was controlled by wolf predation (McLaren and Peterson 1994). When the wolf population declined for any reason, moose reached high densities and suppressed fir growth. Research elsewhere suggests elk populations not regulated by large predators negatively affect the growth of aspen (*Populus tremuloides*) (Kay 1990; Kay and Wagner 1994; Kay 1997; but see Barnett and Stohlgren 2001). Wolves are a significant predator of elk, and wolves may positively influence aspen overstory through a trophic cascade caused by reducing elk numbers, modifying their movement, and changing elk browsing patterns on aspen (White et al. 1998). Ripple and Larson (2000) reported that aspen overstory recruitment ceased when wolves disappeared from Yellowstone National Park.

Climatic patterns, such as El Niño or La Niña, affect the relationship of wolves and ungulate prey (Ballard and Van Ballenberghe 1997; Post et al. 1999). In years that the North Atlantic Oscillation produced deep snow cover, moose were more vulnerable to wolf predation (Ballard and Van Ballenberghe 1997; Post et al. 1999). Thus, the fir forest of Isle Royale was released from heavy browsing, more seedlings were established, more saplings survived, and litter production and nutrient dynamics were affected (Post et al. 1999).

POPULATION DYNAMICS

Many processes are involved in the dynamics of wolf populations. Included are limitations of habitat, environmental variation that causes regular or episodic fluctuations in reproduction; dispersal; intrinsic processes such as demographic stochasticity, effects of age structure, and social system (Vucetich et al. 1997); and genetics (Peterson et al. 1998). The effect of food on wolf populations is mediated by intrinsic social factors, including pack formation, territorial behavior, exclusive breeding, deferred reproduction, intraspecific aggression, dispersal, and primary-prey shifts (Packard and Mech 1980). Population dynamics, however, are primarily dictated by per capita amount of ungulate prey (Keith 1983; Messier and Crète 1985; Fuller 1989; Messier 1994; Eberhardt 1997, 1998; Eberhardt and Peterson 1999) and secondarily by the vulnerability of ungulates to predation (Boertje and Stephenson 1992), disease (see below), level of human-caused mortality (Keith 1983; Fuller 1989), and human activities that displace wolves and their prey from critical habitats (Thiel 1985; Fuller et al. 1992; Paquet et al. 1996; Mladenoff et al. 1995). Any one of these factors, however, can predominate at different times and may interact synergistically with other influences. In addition, the weakening of one factor may enhance another.

Boertje and Stephenson (1992) concluded that wolf productivity declines as prey availability per wolf declines. However, significant declines in reproductive potential only occur when ungulate biomass per wolf declines below threshold levels. Eberhardt and Peterson (1999) estimated an equilibrium ratio for wolves and ungulates of 122 deer-equivalents per wolf. Messier (1987) concluded that in wolf–moose ecosystems with <0.4 moose/km^2, wolves would struggle to subsist, the habitat would not be saturated, and pack sizes would be relatively small with few or no extra adults physiologically capable of breeding. Messier (1985b) estimated that, with moose as the sole ungulate present, minimum prey biomass for a pack to maintain itself is equivalent to a density of 0.2 moose/km^2. In the Superior National Forest, where prey were scarce and the wolf population was declining from high densities, litter size and pack size were inversely related. In the Beltrami Island State Forest, where prey were relatively abundant and the wolf population was increasing, pack size and litter size were positively correlated (Harrington et al. 1983).

Limiting and Regulatory Factors. Limiting factors are density independent, such as the effects of climate on growth rates, whereas regulatory factors are density independent, such as density-induced starvation (Sinclair 1989). Several factors have been reported to limit or regulate growth of wolf populations. These include ungulate biomass (Carbyn 1974; Van Ballenberghe and Mech 1975; Fuller and Keith 1980; Packard and Mech 1980; Keith 1983; Messier 1985a, 1985b, 1987; Peterson and Page 1988), disease (see below), and human-caused mortality (Gasaway et al. 1983; Keith 1983; Peterson et al. 1984; Fuller 1989; Ballard et al. 1987, 1997; Van Ballenberghe 1991; Paquet et al. 1996; Noss et al. 1996).

Quantifying the importance of food in limiting population growth based on cause of death alone is difficult. Results vary among studies. On Isle Royale, annual mortality from starvation and intraspecific strife (both related to low food availability) ranged from 18% to 57% during a 20-year period (Peterson and Page 1988). In populations where some human-caused mortality occurs and thus compensates for natural mortality (starvation, accidents, disease, and intraspecific strife), about 8% of individuals >6 months of age can be lost each year (Ballard et al. 1987; Fuller 1989). Some researchers have accepted this variability and decided any sign of starvation among adult wolves means food is limiting population growth (Fritts and Mech 1981; Ballard et al. 1997). This assumption is reasonable, since adults typically are the last members of the population affected by food shortage (Eberhardt 1977). As such, they may be the most sensitive indicators of food shortages.

Several researchers have suggested that wolf numbers stabilize at a limiting population density. Saturation is thought to occur at about 1 wolf/26 km^2 (Pimlott et al. 1969; Mech 1970), where social behavior

is believed to make space a limiting factor and thereby regulate wolf populations at levels below the level that would adversely affect food resources. Accordingly, territoriality would regulate the number of breeding units and social dominance would limit the number of breeders within each unit. Another theory is that wolf numbers are not limited by territoriality, but exceed the supposed saturation level of 1 wolf / 26 km^2, and wolves continue to prey on available biomass to a point of diminishing returns (Packard and Mech 1980). Wolf numbers at one point reach high densities, and wolves continue to exert heavy losses on prey; this, together with other mortality factors, inevitably results in prey declines, and local extinctions are thought to result (Mech and Karns 1977). With the loss of food, wolf numbers also decline and under favorable conditions prey numbers increase, followed by increases in wolves, and the cycle repeats. Because of lag phases, the wolf–prey systems are perceived to stabilize at different equilibria and follow cyclical predator–prey oscillations. This view seems to have support in the technical literature. It is likely that neither view is applicable in all situations and combinations may occur. Dynamics of multiple-prey systems are further complicated because of the potential for prey switching and opportunistic predation (Seip 1992).

The rate of annual mortality that controls growth of wolf populations is unknown. Mech (1970) concluded an annual harvest (hunting or trapping) of 50% or more was necessary to control wolf populations based on pup–adult ratios, but did not distinguish between harvest and natural mortality. However, Keith (1983) and Fuller (1989) reviewed numerous wolf studies across North America and concluded that harvests exceeding 28–30% of fall populations resulted in declines. Fuller (1989) further concluded that populations would stabilize with an overall annual mortality rate of 35%. Peterson et al. (1984) and Fuller (1989) found evidence that harvest effects vary with time and population structure. For instance, if productivity is high, and consequently so is the ratio of pups to adults, the population can withstand a higher overall mortality because pups (nonproducers) make up a disproportionately larger amount of the harvest (Fuller 1989). Furthermore, net immigration or emigration may mitigate the effects of harvest (Fuller 1989). Multiple denning within individual packs (Harrington et al. 1982; Ballard et al. 1987) can also have a significant influence on rates of increase and sustainable mortality rates.

Ballard et al. (1997) reviewed three factors (pack size, number of pups, and multiple denning) that they felt determined the amount of mortality populations of wolves can withstand. Wolf populations comprising small wolf packs can withstand higher levels of exploitation than those comprising large packs, provided that reproductively active females are not killed. Populations with high proportions of pups can also withstand heavier exploitation than populations comprising large proportions of adults because pups are more vulnerable to exploitation and in populations with fewer pups, adults may make up a larger proportion of the harvest (Fuller 1989).

Rates of Growth.   Three factors dominate wolf population dynamics: wolf density, ungulate density, and human exploitation. These are linked through wolf predation, social behavior, and functional and numerical responses. Rate of increase and densities in wolf populations are primarily a function of ungulate biomass and secondarily age structure of the population and human-caused mortality. In most cases, stable wolf populations are in equilibrium with their ungulate prey (Keith 1983). Reported rates of growth in wild wolf populations have varied between 0.93 and 2.40 (Fuller and Keith 1980; Fritts and Mech 1981; Ballard et al. 1987; Fuller 1989; Hayes et al. 1991; Messier 1991; Pletscher et al. 1997). Few, if any, populations achieve a theoretical exponential rate of 0.833 ($\lambda = 2.30$) given maximum reproduction (Rausch 1967), a stable age distribution, and no deaths. Keith (1983), calculated a maximum rate of increase ($r = 0.304$, $\lambda = 1.36$) based on the highest reproductive and survival rates reported from studies on wild wolves. The rate of increase of different populations likely varies with environmental and ecological factors.

Wolf populations can compensate demographically for excessive mortality. Under certain circumstances, this compensation enables wolves to respond to increased rates of juvenile or adult mortality with increased reproduction and/or survival, thereby mitigating demographic fluctuations (Weaver et al. 1996). Dominant wolves can reproduce at a very young age and usually reproduce every year after that (Weaver et al. 1996). Age at reproductive senescence has not been well documented, but few females survive to reproduce past the age of nine years (Mech 1988). Wolves also display remarkable ability to recover from exploitation. Human-induced mortality in wolf populations tends to reduce wolf densities, which alters predator–prey ratios (i.e., more prey per predator), which in turn raises rates of increase.

MORTALITY

Causes of Mortality.   Wolves die because of accidents (Fuller and Keith 1980; Boyd et al. 1992), starvation (Mech 1972; Seal et al. 1975; Van Ballenberghe and Mech 1975; Mech 1977b; Fuller and Keith 1980), intraspecific strife (Mech 1972; Van Ballenberghe et al. 1975; Messier 1985a, 1985b; Ballard et al. 1987), interspecific conflicts (Stanwell-Fletcher 1942; Frijlink 1977; Ballard 1980, 1982; Nelson and Mech 1985; Mech and Nelson 1990; Weaver 1992), disease (see above), and human-related causes. Causes of human-related mortality includes legal harvest (Fuller and Keith 1980; Gasaway et al. 1983; Keith 1983; Peterson et al. 1984; Messier 1985a; Ballard et al. 1987, 1997; Potvin 1987; Bjorge and Gunson 1989; Fuller 1989; Hayes et al. 1991; Pletscher et al. 1997), illegal harvest (Fritts and Mech 1981; Fuller 1989; Pletscher et al. 1997), vehicles on highways (Berg and Kuehn 1982; Potvin 1987; Fuller 1989; Forbes and Theberge 1995; Thiel and Valen 1995; Bangs and Fritts 1996; Paquet and Callaghan 1996; Paquet et al. 1996), trains (Paquet 1993; Paquet et al. 1996; Krizan 1997; Forshner 2000), and introduced diseases (see above).

Researchers have noted that starvation and intraspecific aggression are more common when wolves are faced with a low density of prey (Van Ballenberghe and Erickson 1973). For instance, Messier (1985b) reported that in southwestern Quebec, the mortality rate of wolves living in an area with low densities of prey was higher than the rate for wolves living in an area of high densities of prey. This was because wolves with less prey incurred more deaths from starvation and intraspecific aggression. Similarly, Mech (1977a) found that intraspecific aggression increased as prey availability declined in Minnesota. However, Mech (1977a) tasael that only pups seemed to starve. Other investigators have also reported that a shortage of prey increases natural mortality (Van Ballenberghe and Mech 1975; Mech 1977a; Messier 1985b).

Wolves risk injury (Rausch 1967; Phillips 1984; Pasitschniak-Arts et al. 1988) and death in attempting to kill large prey (Mech 1970). Healthy, vigorous prey often escape wolf predation by fighting back or fleeing (Mech 1984; Nelson and Mech 1993; Stephenson and Van Ballenberghe 1995). Weaver (1992) noted that about 25% of 1450 wolves killed by humans in control programs in Alaska showed traumatic skull injuries, presumably inflicted by moose and other large prey. On occasion, moose, bison, elk, and deer can gain the upper hand and kill attacking wolves (Stanwell-Fletcher 1942; Frijlink 1977; Nelson and Mech 1985; Mech and Nelson 1990; Weaver 1992). The risk to wolves appears to increase with size of prey. Several wolf–moose studies have shown that wolves often search for less risky opportunities rather than attack such dangerous prey (Stephens and Krebs 1986; Forbes 1989). Avalanche-caused wolf mortality has been reported in Alberta (Boyd et al. 1992) and Alaska (Mech et al. 1992 in Boyd et al. 1992). Wolves also are killed occasionally by other predators (see below).

Diseases.   Many authors have concluded that food abundance by itself, or in combination with social stress, is the main regulatory factor of wolf populations. Diseases, however, can be important modulators of the many processes that determine population dynamics of wolves (Carbyn 1982a; Bailey et al. 1995). A wolf pack may be affected by disease through loss of experienced adults, reduced recruitment of young, and decimation or disruption of pack social structure. Disease has not been linked to low food availability, but the relationship makes sense

intuitively. A population of wolves that suffers from lack of food should be more vulnerable to disease than a population with more food available. Furthermore, food shortage leading to nutritional stress may combine with disease factors to increase the significance of otherwise innocuous or sublethal conditions (Brand et al. 1995).

Diseases of wolves have been summarized (Mech 1970; Custer and Pence 1981; Brand et al. 1995), but the affects of epizootics and enzootics on the dynamics of wolf populations have not been well documented. Most studies report no disease-related or disease-caused deaths of wolves (Van Ballenberghe et al. 1975; Mech 1977a; Fritts and Mech 1981; Messier 1985b; Potvin 1987; Ballard et al. 1987; Hayes et al. 1991; Meier et al. 1995; Pletscher et al. 1997). Where documented, from 2% to 21% of wolf mortality has been attributed to disease (Carbyn 1982a; Peterson et al. 1984; Fuller 1989; Ballard et al. 1997). The transmission of disease, such as parvovirus, from domestic dogs to wild wolves is a serious conservation concern (Bailey et al. 1995).

Rabies is an important zoonosis, but is infrequently reported in wolves (Cowan 1949; Rausch 1958; Chapman 1978; Theberge et al. 1994). Ballard et al. (1997) concluded that rabies was a significant factor in a decline of wolves from Alaska. In that study, rabies-caused mortality was 21%. Little is known about the effects of bacterial zoonoses on wolf populations. Wolves are definitive hosts for various protozoan infections. The most notable are toxoplasmosis and sarcosporidosis. Although numerous arthropod parasites are known, only sarcoptic mange is an epizootic disease of significance. There is little evidence that non-infectious deseases are serious problems in the morbidity and mortality of wolves. In contrast, many infectious disease agents have been reported. Some of these reach epizootic proportions and occasionally affect their populations. Important viral infections thought to be significant are distemper and canine hepatitis (Custer and Spence 1981; Brand et al. 1995). Other diseases that occur in wolf populations are canine parvovirus (Mech and Goyal 1993, 1995; Johnson et al. 1994; Bailey et al. 1995; Mech et al. 1997), Lyme disease (Kazmierczak et al. 1988; Thieking et al. 1992), heartworm (*Dirofilaria immitis;* Mech and Fritts 1987), leptospiroseus, blastomycosis (Thiel et al. 1987; Krizan 2000; Paquet et al. 2001a), tuberculosis (Carbyn 1982a), and coccidiosis (Mech and Kurtz 1999). The effects of these diseases are largely unknown.

Murie (1944) discussed mange, canine distemper, and rabies as possible regulating factors in Alaskan wolf populations. Distemper and mange may have reduced wolf populations in Jasper National Park during the 1940s (Carbyn 1982a). Sarcoptic mange is an important, sometimes common, but rarely reported disease of wolves (Todd et al. 1981), caused by a mite, *Sarcoptes scabiei*. Based largely on circumstantial evidence, several researchers believed that mange is an important regulating factor in wild canid populations (Pike 1892; Murie 1944; Cowan 1951; Green 1951; Todd et al. 1981). For example, during a 10-year period in Alberta, mange was present in wolves each year, but the number of cases increased when wolf densities increased, and the number of pups surviving decreased as prevalence of mange increased (Todd et al. 1981). Todd et al. (1981) found that weights of xiphoid-process fat globules of mangy coyotes and wolves were lower than weights from nonmangy animals although many animals were lightly infested. In addition, body weights of mangy wolves averaged 4–10% less than weights of nonmangy wolves.

BEHAVIOR

Social Behavior and the Pack. Although some wolves are solitary, most are highly gregarious and live in packs with complex social structures. Pack size is largest in fall and early winter when pups are integrated into the pack. Reductions in pack size by late winter are typically due to pup and adult mortality as well as dispersal of younger wolves. Wolf packs are usually made up of 5–12 individuals, although larger packs may be found (Mech 1974). For example, Mech (2000) documented a pack of 22–23 wolves in central Minnesota. Because the pack preyed primarily on white-tailed deer, he cited this as evidence

that prey size and pack size are not tightly linked (see discussion below). Packs in the Northwest Territories of Canada occasionally coalesce into groups of 20–30 animals when hunting bison (Carbyn et al. 1993). A pack of 28 individuals in spring and a pack of 40 in autumn were observed in association with migratory barren-ground caribou (F. Miller, Canadian Wildlife Service, Edmonton, Alberta, pers. commun., 1999).

The proximal mechanism underlying the regulation of pack size is complex and imperfectly understood (Zimen 1976, 1982; Packard and Mech 1980; Haber 1996a). An increase in prey abundance seems to produce a direct increment in the in-group recruitment and survival rates (Keith 1983). As prey abundance increases, the territory mosaic becomes progressively saturated (lower territory vacancy), which could provoke delayed dispersal (Packard and Mech 1980; Messier and Barrette 1982; Messier 1985a). Nudds (1978) detected an apparent relationship between wolf pack size and food acquired per wolf, which implied that packs smaller than optimal size acquired substantially less food per wolf than those of optimal size. He also speculated that there were different optimal pack sizes for wolves preying on moose and other large prey than for those preying principally on deer. However, Thurber and Peterson (1993) demonstrated that for wolves preying primarily on moose on Isle Royale, food acquisition per wolf decreased with increased pack size. Hayes (1995) reported the same for wolves preying on moose and caribou. Dale et al. (1995) concluded that the larger packs killing moose, caribou, and Dall sheep (*Ovis dalli*) acquired no more food per wolf than smaller packs. A comprehensive review of prey use by wolves in several geographic areas showed a negative relationship between pack size and food acquisition per wolf (Schmidt and Mech 1997). Taken together, these studies provide strong evidence against the idea that wolves live in packs to facilitate predation on large prey.

The pack is usually a breeding pair and their offspring of the previous 1–3 years, or sometimes two or three such families (Murie 1944; Young and Goldman 1944; Mech 1970 1988; Clark 1971; Haber 1977; Mech and Nelson 1989). Most offspring disperse near 3 years of age (Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987; Fuller 1989; Gese and Mech 1991). Although female wolves in captivity have bred successfully at 10 months of age (Medjo and Mech 1976), wild wolves typically do not breed until at least 22 months (Rausch 1967; Mech 1970). Occasionally, an unrelated wolf is adopted into a pack (Van Ballenberghe 1983a; Lehman et al. 1992; Mech et al. 1998) or a relative of a breeder is included (Haber 1977; Mech and Nelson 1990; Mech et al. 1998), or a dead parent is replaced by an outside wolf (Rothman and Mech 1979; Fritts and Mech 1981; D. Smith, National Park Service, Yellowstone National Park, Wyoming, pers. commun., 2000). In the latter case, an offspring of opposite sex from the newcomer may replace its parent and breed with the stepparent (Fritts and Mech 1981; Mech and Hertel 1983).

Communication is through postures (Schenkel 1947, 1967; Crisler 1958; Fox 1971, 1973, 1975; Zimen 1976, 1982; Fox and Cohen 1977), vocalizations (Harrington and Mech 1978a, 1978b, 1979, 1983; Harrington 1986, 1989; Coscia et al. 1991; Coscia 1995), and scents (Kleiman 1966; Theberge and Falls 1967; Peters 1978; Harrington 1981; Asa et al. 1985a, 1985b; Merti-Millhollen et al. 1986; Paquet 1989; Asa 1997; Asa and Valdespino 1998). All wolves exhibit similar behaviors, although a degree of individual variability exists (Fox 1975; Zimen 1982). Fixed patterns of behavior express the inner state of a wolf to which other wolves respond. As with domestic dogs, an elevated tail and erect ears convey alertness and sometimes aggression. Facial expressions, emphasized by the position of the lips and display of the teeth, are the most dramatic form of communication. Scent from urine and possibly fecal matter is used to express social status and breeding condition and advertise territorial occupancy (Peters and Mech 1975, 1978; Asa et al. 1985a). A gland at the ventral base of the tail and anal glands may also exude chemicals used in communication (Asa et al. 1985b).

Wolves organize themselves into strict dominance hierarchies where individual position reflects status and privilege. Details of social structure vary with the number, sex, age, and reproductive structure

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of the group. In large packs, males and females have separate linear hierarchies in which each animal knows its position (Zimen 1976, 1982). At the top of these hierarchies are the highest ranking male and female, one of which serves as alpha wolf or pack leader. Females are as likely to lead the pack as males. Interactions between the sexes are more complex because of breeding relationships. Rank positions are not permanent and agonistic contests are most intense during the winter breeding period (Peterson 1979).

A few people have observed the social behavior of wild wolves around dens. Murie (1944) gave an anecdotal account. Clark (1971) presented a quantified summary of the pack social relationships. Haber (1977) described his interpretation of a pack's social hierarchy without supporting evidence. Based on summer observations of wolves on Ellesmere Island, Mech (1999b) described the wolf pack social order, the alpha concept, and social dominance and submission. He concluded that adult parents guide the activities of the pack in a division of labor system. The female predominates primarily in such activities as pup care and defense, and the male primarily during foraging and food provisioning.

The complex social organization found within and between wolf packs may have subtle influences on physiology and behavior that are of regulatory importance (Haber 1996a). Social relationships within the pack may also be sensitive to food supply and thus influence size of a pack. The most common explanation for the highly evolved social behavior of wolves is the need for cooperation in hunting large prey (Murie 1944; Mech 1970; Zimen 1976; Peterson 1977; Nudds 1978; Pulliam and Caraco 1978; Rodman 1981), although even single wolves can kill prey the size of moose (Thurber and Peterson 1993) and bison (Carbyn and Trottier 1988; Carbyn et al. 1993). An alternative view proposes that wolves live in packs so adult pairs can efficiently share with their offspring surplus food resulting from the pair's predation on large mammals (Schoener 1971; Rodman 1981; Hayes 1995; Schmidt and Mech 1997). A social capacity limit independent of food supply may also influence group size (Mech 1970; Zimen 1976; Packard 1980; Packard and Mech 1980; Packard et al. 1983, 1985).

Chemical and Vocal Communication. Scent markings and vocalizations are used by wolves to maintain territories and communicate among themselves. For territorial advertisement, vocalizations are thought to be less important than scent marking (Harrington and Mech 1978b, 1983). Scent marking is long term and site specific, whereas howling is immediate and long range (Harrington and Mech 1979). Distinctive howling (Joslin 1967, Harrington and Mech 1978b) and the presence of recent urine marks may limit direct aggression between packs by encouraging wolves to avoid alien territories (Peters and Mech 1975). Scent marking involves urine (Raymer et al. 1984, 1986), feces, and anal scent glands (Kleiman 1966; Ewer 1973; Raymer et al. 1985; Asa et al. 1985a, 1985b), often in conjunction with scratch marks (Paquet 1991a). Scent rubbing may also be involved in communication (Harrington et al. 1986). The raised-leg urination of wolves is generally accepted as a form of scent marking (Kleiman 1966; Ewer 1973). Scent marking may play a role in intrapack communication by expressing sex, reproductive state (Ryon and Brown 1990), and dominance (Macdonald 1985). Establishment and maintenance of pair bonds may also involve scent marking (Rothman and Mech 1979).

Urine Marking. Time spent in each part of a territory influences the frequency of urine marking (Paquet and Fuller 1990; P. Paquet, unpublished data). Accordingly, the number of marks could be elevated in areas of high prey density as a reflection of foraging behavior by wolves (Paquet and Fuller 1990). Physiography also influences the frequency and distribution of scent marking (Peters and Mech 1975; Paquet 1991a). In winter, established roads and trails exhibit the highest number of marks and frozen water bodies the lowest. Therefore, territories encompassing large bodies of water and/or unusual configuration of roads and trails might show an uneven representation of scent marks.

Wolves increase their rate of scent marking when they encounter scent marks from members of other packs (Peters and Mech 1975).

The fresher the scent mark, the more likely it is to elicit another mark (Paquet 1989). Dominant wolves mark more than subdominants, and female wolves mark more than males (Haber 1977; Asa et al. 1990; Ryon and Brown 1990). Nonbreeding wolves seldom scent mark (Rothman and Mech 1979), whereas newly formed pairs mark the most (Rothman and Mech 1979). Lone wolves rarely mark (Rothman and Mech 1979; Paquet 1991a). Urine marks of female wolves are responded to more frequently than those of males. Visual display, used in conjunction with urine marking, may play a role in interpack communication by signaling dominance. Marking frequency of female wolves increases during courtship and breeding season, and the response of other wolves to the marks of females also increases during these periods (Ryon and Brown 1990). Because the volatile chemical constituents of the urine of male and female wolves change seasonally (Raymer et al. 1984, 1986), urine marks may also provide information on reproductive status. Urine is also used to mark caches of food (Harrington 1981).

Peters and Mech (1975) concluded that wolf-marking sites are more numerous along territorial borders, and proposed as a model an "olfactory bowl" of scent, in which the number of marks decreases from the edge to the middle of a territory. In theory, this higher density of scent marks enables packs to recognize the periphery and keep from trespassing into more dangerous areas beyond. Barrette and Messier (1980), however, questioned the appropriateness of the model because it was based on marks/km rather than marks/km^2. Moreover, wolf packs in Riding Mountain National showed no difference between peripheral and interior marking rates, although scent marks were more abundant in some areas than others (Paquet and Fuller 1990).

Howling. Howls can be heard for several kilometers under certain conditions. Joslin (1967) reported that howling could advertise the presence of wolves over a 130-km^2 area. Spontaneous and elicited howls are influenced by time of year and social circumstances (Harrington and Mech 1978a, 1978b). Rate of howling by two wolf packs in Minnesota increased throughout the pup-rearing season (Harrington and Mech 1978a). Wolves characteristically respond to human disturbance near their pups by barking and howling (Chapman 1977). A midwinter increase in howling is associated with reproductive behavior, especially for groups containing breeding animals. Through the year, the rate of elicited howling is higher among packs and lone wolves attending kills. The more food remaining at a kill, the higher the rate of reply. Larger packs reply more often than smaller packs. Lone wolves rarely reply, reflecting the low-profile behavior expected of surplus animals in territorial populations. The responsiveness of lone wolves depends on the status of the wolf before becoming a loner and amount of time since it left the pack. For wolves separated from their pack, the howling reply rate depends on their age and social role. Dominant adults are more likely to howl than subordinate younger animals. Howling may reflect the status and motivational state of wolves. Harrington (1987) reported that howls of antagonistic wolves were deeper in pitch than those of passive animals. He speculated that during aggressive encounters, use of low-frequency, harsh sound expresses body size, which is a primary determinant in the outcome of aggressive interactions. Although animals of larger size can produce sounds of lower pitch and harsher tonal quality, size can be exaggerated by vocal manipulation.

Howling may be involved in coordination of pack activities (Harrington and Mech 1978b). Harrington (1975) reported that howling is important in maintaining pack structure in populations of high mortality, helping to assemble individuals after they have been separated. On Isle Royale, howling was important in coordinating moves of a large pack (Peterson 1977). Most howling was heard at night when adults were hunting and spatially separated. Such howling may help wolves synchronize hunting efforts. Carbyn (1975a) recorded crepuscular peaks in howling at wolf rendezvous sites in Jasper National Park, Alberta. Increased howling at dawn and dusk may be associated with departures and arrivals of adults at rendezvous areas (Harrington and Mech 1978a, 1978b).

ECONOMIC STATUS, MANAGEMENT, AND CONSERVATION

Viable, well-distributed wolf populations depend on abundant, available, and stable ungulate populations. Flexible feeding habits, high annual productivity, and dispersal capabilities enable wolves to respond to natural and human-induced disturbances (Weaver et al. 1996). Though evidence is lacking, movement among many North American subpopulations of wolves appears relatively unimpeded and, for the most part, the current rate of mortality sustainable. The fate of wolves ultimately depends on our ability to coexist with them at a local level. Therefore, successful management and conservation of wolves depends as much on social acceptance as on protecting the species's biological requisites.

Controlling wolves to protect livestock, enhance ungulate populations, and protect endangered species such as mountain caribou and whooping cranes (Kuyt et al. 1981; Edmonds 1988) for the benefit of humans remains controversial (Archibald et al. 1991; Cluff and Murray 1995; Buss and de Almeida 1998; Haber 1996; Thompson et al. 2000). Most of the debate focuses on the relative contributions of overhunting, industrial development, recreational development, and wolf predation to the decline of ungulates. Currently, wolves are controlled by shooting, poisoning, trapping, and sterilization (Haight and Mech 1997). Wolf control programs have been demonstrated to increase ungulate numbers (Gasaway et al. 1983; Bergerud and Elliott 1986, 1998; Farnell and McDonald 1988), but due to negative public reaction such programs have been delivered at substantial costs to the agencies involved. As noted above, some research suggests wolf predation can have a regulatory affect on ungulates (e.g., Mech and Karns 1977; Gasaway et al. 1983; Larsen et al. 1989; Bergerud and Elliot 1998; Hayes and Harestad 2000b). Less clear, however, is the role of predation in initiating such declines (Gauthier and Theberge 1987).

For the most part, management of wolf populations outside protected areas could be improved (Mech 1995; Thompson et al. 2000). Livestock and wolves need to be managed in areas of conflict. As wolf populations continue to grow in newly colonized or reestablishment areas, there may be an increasing need for control of those wolves preying on livestock (Fritts 1993). Because the public has so strongly supported wolf recovery and reintroduction, understanding the need for control may be difficult for many. Thus, strong efforts at public education will be required. Social approval for protection of livestock and enhancement of subsistence hunting may be higher than for furtherance of sport hunting. In addition, public acceptance of methods used to reduce wolf populations varies regionally and culturally.

In most of North America, regional wolf populations require core wilderness areas to persist (Mladenoff et al. 1995, 1999; Paquet et al. 1996; Woodroffe 2000; Carroll et al. 2001; Callaghan 2002). In this human-dominated world, however, requirements of the wolf are quickly becoming rare commodities. Insert even the largest North American parks and reserves are inadequate in area to fully protect wolves (Woodroffe and Ginsberg 1998). Packs living in highly productive environments such as Yellowstone National Park require about 150–300 km^2. In mountainous areas, annual home ranges can be as large as 3000 km^2 (Paquet et al. 1996). Wolves living in the Arctic, which depend on caribou, may use areas of 60,000 km^2 or larger (Walton et al. 2001). The number of protected areas should be increased in some areas and the effectiveness of existing reserves that are too small, or have unsuitable configurations, could be improved by the creation of buffer zones.

In many parts of North America, wolves live in networks of disjunct populations, many of which are close to human settlement. Wolves can survive in disjunct populations if movement between populations is unobstructed, human persecution is not excessive, and prey is abundant (Haight et al. 1998). Wolves do move throughout human-occupied landscape, across many unfavorable areas, but establishment success is restricted to higher quality habitat characterized by low human presence.

Population Status. The status of the gray wolf in its global range (North America, Eurasia, and the Middle East) is listed as vulnerable (Hilton-Taylor 2000). The North American gray wolf was added to

TABLE 23.2. Estimates of adult wolf populations in the United States and Canada

State/Province/Territory	Trend	Population Estimate
Newfoundland/Labrador	Increasing	1,500
Quebec	Stable	4,000
Ontario	Stable	8,000–10,000
Manitoba	Stable	4,000–6,000
Saskatchewan	Undetermined	2,000–4,500
Alberta	Decreasing	3,000–5,000
British Columbia	Stable	4,000–8,000
Northwest Territories and Nunavut	Stable, declining on Queen Elizabeth Islands	10,000
Yukon	Stable	4,500
Michigan (Upper)	Increasing	100
Michigan (Isle Royale)	Oscillating	10–25
Wisconsin	Increasing	100
Minnesota	Stable	2,500
North Dakota	Dispersers, no resident population	<10
Montana (northern)	Stable	63
Wyoming/Montana (Greater Yellowstone)	Increasing	170
Arizona/New Mexico	?	30–40
Idaho	Increasing	192
Oregon	Dispersers, no resident population	<10
Washington	?	<10
Alaska	Stable	6,000–7,500
Total		50,000–55,000

SOURCE: United States, Bangs et al. (2001). Canada, Van Zyll De Jong and Carbyn (1999).

Appendix II of the Convention on the International Trade in Endangered Species of Wild Flora and Fauna (CITES) in 1977. That agreement regulates international trade of animals and plants when that trade (1) threatens the species survival or the survival of a geographic population of that species or (2) the species looks like a threatened species. The North American gray wolf was listed under CITES to help control trade of endangered gray wolf populations in other parts of the world, not because the species is threatened or endangered globally.

Because of diversity in climate, topography, vegetation, human settlement, and development, wolf populations in various parts of the original North American range vary from extirpated to pristine. As of March 2002, the species is listed as threatened in Minnesota and endangered (U.S. Endangered Species Act) in states other than Alaska. Review of the current status of all wolf populations in contiguous states is under way (U.S. Fish and Wildlife Service 2000). All Canadian populations are unlisted (Matthews and Moseley 1990). Note, however, that Canada lacks endangered species legislation at the federal level. Newly proposed taxonomic classifications and the success of reintroduction programs may require a reassessment of North American wolf populations (Wilson et al. 2000).

The estimated population of gray wolves in North America is about 50,000 (Table 23.2). An estimated 3000 wolves occupy the lower 48 states and approximately 6500 wolves inhabit Alaska. All wolf populations in the contiguous 48 states are increasing, whereas populations in Alaska are stable. Several new populations have become established in Montana, Wyoming, and Idaho through natural recolonization and reintroduction of wild-caught Canadian wolves (U.S. Fish and Wildlife Service 1987; Bangs and Fritts 1996; Bangs et al. 1998, 2001). Natural expansion into (Licht and Fritts 1994) Washington, Oregon, and California is probable (Carroll et al. 2001). Reintroduction of captive-bred Mexican wolves into Arizona is currently under way (U.S. Fish and Wildlife Service 1982; García-Moreno et al. 1996; Parsons 1998; Kalinowski et al. 1999; Brown and Parsons 2001; Paquet et al. 2001c). Additional reintroductions are being considered for northeastern United States (U.S. Fish and Wildlife Service 1987; Wydeven et al. 1998; Harrison and Chapin 1998; Mladenoff and Sickley 1998; Paquet et al.

2001b) and Colorado. In Minnesota, wolves occupy all suitable areas and have begun to colonize agricultural regions (U.S. Fish and Wildlife Service 1992). The occupied range of wolf populations and numbers of wolves in Wisconsin and Michigan are expanding. The number of gray wolves in Canada is estimated at 50,000–60,000 (Theberge 1991; Carbyn 1994), occupying 80% of their former range. The status of populations in the High Arctic is unknown because inventory and survey records are not available. Moreover, the area is huge and largely uninhabited by people. Canadian wolf populations most sensitive to human activities and/or natural events are the eastern wolf (*C. l. lycaon*), high arctic wolf (*C. l. arctos*) (van Zyll De Jong and Carbyn 1999), and all wolves inhabiting coastal islands.

Economic Status. Systematic economic assessments involving wild wolves are rare (Duffield and Neher 1996; Rasker and Hackman 1996). Most government agencies responsible for management of wolves have not conducted such analyses. Incomplete information is occasionally buried in reports but lacks the economic context necessary for evaluation. The emphasis is usually on financial costs incurred in lethal management of wolves to reduce predation on livestock and wild ungulates (Wagner et al. 1997). Costs and benefits associated with the sale of wolf fur are seldom available. Potential biological costs and ecological benefits of managing wolves are seldom quantified. Mech (1998), for example, evaluated the financial costs of wolf management options, but did not consider possible monetary benefits or other less tangible values. Clearly, comprehensive and rigorous economic evaluations are necessary for informed management decisions.

Good economic information is also needed to counter market forces that encourage destruction of formerly secure wolf habitats. Over the last 200 years, the North American landscape has been modified by an economy that ignores the environment or views it as an obstacle to overcome. Within this context, the decline of wolves has been considered a measure of the success of an enterprising economy. This attitude continues to prevail because only monetary benefits and costs associated with resource products are recognized in conventional marketplace transactions. Whereas conservation and restoration efforts are directed at improving current and future conditions, market interests usually discount future benefits and costs in favor of present consumption. Because information about the future is limited, a premium is placed on the present. Accordingly, short-term profits are usually favored over the uncertain profits of the future. Wolves can help society come to terms with the total value of biological diversity because their presence causes us to consider the comparative value of tangible and intangible aspects of the things that make up our lives (Pimlott et al. 1969).

Response of Wolves to Humans. To assess the effects of human influence accurately, we must know the uninfluenced norms and ranges. Because such information is lacking, the degree of influence by humans is imperfectly understood. Interpretation of the wolf–human interaction is confounded by multiple factors that influence how wolves use the landscape and respond to people (Mladenoff et al. 1995; Fritts and Carbyn 1995; Paquet et al. 1996; Carroll et al. 2001; Duke et al. 2001). The extent and intensity of response appear to vary with environmental conditions, social context, and disturbance history. Disturbance history is a critical concept in understanding the behavior of long-lived animals that learn through social transmission (Curatolo and Murphy 1986). Given the wolf's inherent behavioral variability, it is unlikely that all individuals, packs, or populations react equally to human-induced change or humans. Because researchers have developed no reasonable expression of individual differences, our understanding of wolf/human interactions is limited to the pack and population levels (Mladenoff et al. 1995, 1997, 1999; Paquet et al. 1996; Boyd-Heger 1997; Mladenoff and Sickley 1998; Carroll et al. 2001; Callaghan 2002).

Specific conditions that impair the distribution, movements, survival, or fecundity of wolves are believed to be highly variable. Although wolves are sensitive to human predation and harassment (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller 1989; Mech 1989, 1993, 1995; Fuller et al. 1992; Thurber et al. 1994; Mladenoff et al. 1995,

1999; Paquet et al. 1996), we have limited empirical information on tolerance to human disturbance. Reactions of wolves to people likely depend on the type of human activity, where the interaction occurs, the distance between the activity (person) and the animal, cover, a wolf's experiences, inherited tolerance, and age/sex class. Wolves can habituate to human activities, at least partially, provided these activities are repetitive and innocuous. A wolf's experience with humans is important because habituation affects the wolf's sense of security. Studies have shown wolves avoid humans in time (Boitani 1982) and space (Mladenoff et al. 1995; Paquet et al. 1996) or are displaced via human-induced mortality (Paquet et al. 1996; Duke et al. 2001). Although human activities influence the distribution (Thiel 1985; Fuller et al. 1992; Paquet et al. 1996; Mladenoff et al. 1995) and survival of wolves (Mech et al. 1995b; Mladenoff et al. 1995; Fritts and Carbyn 1995; Paquet et al. 1996), human-caused mortality is consistently cited as the major cause of displacement (Fuller et al. 1992; Mech and Goyal 1993; Fritts and Carbyn 1995; Bangs et al. 2001).

Recent reports suggest wolves in Minnesota tolerate higher levels of disturbance than previously thought possible. Wolves, for example, are now occupying ranges formerly assumed to be marginal because of prohibitive road densities and high human populations (Mech 1993, 1995). Legal protection and changing human attitudes are cited as the critical factors in the wolf's ability to use areas that have not been wolf habitat for decades. Several studies suggest adequate prey density is the main factor limiting wolves where they are present and tolerated by humans (Keith 1983; Fuller et al. 1992; Mech 1993, 1996; Fuller and Murray 1998). If wolves are not persecuted, they seem able to occupy areas of greater human activity than previously assumed (Fuller et al. 1992; Mech 1993; Fritts et al. 1994; Fritts and Carbyn 1995). Based on these observations, Mech (1995) commented that misconceptions about the gray wolf's inherent ability to tolerate human activity encourage unwarranted protectionism.

Nonetheless, wolves continue to occur most often where road density and human population are low (Fuller et al. 1992; Mladenoff et al. 1995; Paquet et al. 1996; Callaghan 2002). Gray wolves from the Great Lakes region of the United States and Canada may have hybridized with coyotes (Kolenosky 1971; Schmitz and Kolenosky 1985a, 1985b; Schmitz and Lavigne 1987; Wayne et al. 1991, 1992; Lehman et al. 1991; M. T. Theberge et al. 1996) and red wolves (Wilson et al. 2000; Fascione et al. 2001), which may affect their behavior (Fox 1971, 1975) and their relationship with humans. Consequently, extrapolating information from Minnesota, Michigan, Minnesota, and Ontario may be inappropriate for other parts of North America. For example, wolves in the Rocky Mountains show no introgression of coyote genes (Arjo and Pletscher 1999). Moreover, the fact that wolves are using areas of greater human activity suggests dispersers or marginalized individuals and packs are being pushed into lower quality habitats (Mladinoff et al. 1999). This suggests that wolves occupy habitat closer to humans only if necessary to acquire life requisites (Paquet et al. 1996; Woodroffe 2000). A similar phenomenon has been observed with grizzly bears (Mattson et al. 1987). An alternative explanation is that the social flexibility of wolves allows the species to adapt their behavior to survive in human-altered habitats. For example, Eurasian wolves have become more secretive where they coexist with people, adopting a strategy of nocturnal scavenging (Boitani 1992).

Use of Habitats. Essential to any evaluation of the relationship between wolves and humans is an understanding of which habitats are inherently attractive to wolves. A general assumption is that habitat use is strongly related to availability of ungulate prey (Huggard 1991; Keith 1983), ease of travel (Cowan 1947; Mech 1970; Peek et al. 1991; Paquet et al. 1996), availability of den sites (Chapman 1977), and availability of rendezvous areas (Theberge 1969; Carbyn 1975a; Mech 1970). Evidence from field studies strongly suggests that when habitat is high very attractive, wolves move closer to human activities because of the benefit. Conversely, when quality of habitat is low, displacement is greater because security risks outweigh advantages (Boitani 1982; Paquet et al. 1996).

In recent years, researchers have used geographic information systems and spatial radio-collar and wolf occurrence data to assess the importance of landscape-scale factors in defining favorable wolf habitat (Mladenoff et al. 1995, 1999; Paquet et al. 1996; Meriggi et al. 1996; Massolo and Meriggi 1998; Corsi et al. 1999; Callaghan 2002). These and earlier studies (e.g., Meriggi et al. 1991; Fritts et al. 1994; Bangs et al. 1998) agree that an adequate prey base, existence of sufficient protected areas, and absence or low occurrence of livestock are necessary to maintain wolf populations. Wolf presence also depends on areas with forest cover, few roads, and low human density. Wolves thrive in areas with high ungulate densities, but tend toward extirpation in areas with high densities of livestock because of conflicts with ranchers (Bangs et al. 1998). Protected and public lands encourage wolf presence, likely because there are fewer lethal encounters with humans (Forbes and Theberge 1996a). Some authors (e.g., Mech 1995) maintain that such areas are the least accessible to humans, and that the lack of human presence is the most important variable in predicting wolf viability.

We are aware of only five studies that have systematically and explicitly examined the landscape relationship of wolves and humans (Mladenoff et al. 1995, 1999; Paquet et al. 1996; Theberge et al. 1996; Corsi et al. 1999; Callaghan 2002). Observed patterns of displacement suggest the presence of humans repulses wolves, although a strong attraction to highly preferred habitats increases a wolf's tolerance for disturbance. As conditions become less favorable, the quality of habitat likely takes on greater importance. In the northern Great Lakes (Mladenoff et al. 1995), human population density was much lower in pack territories than in nonpack areas. Wolf pack territories also had more public land, forested areas with at least some evergreens, and lower proportions of agricultural land. Notably, no difference was detected between white-tailed deer densities in pack territories and nonpack areas. Overall, wolves selected areas most remote from human influence, with <1.54 humans/km^2 and <0.15 km roads/km^2. Most wolves in Minnesota (88%) were in townships with <0.70 km roads/km^2 and <4 humans/km^2 or with <0.50 km^2 and <8 humans/km^2. In Italy, absence of wolves was related to human density, road density, urban areas, cultivated areas, and cattle and pig density. However, because human density, road density, and urbanized areas were highly intercorrelated, no specific human effect was established (Corsi et al. 1999). In the Bow River Valley, Alberta, the selection or avoidance of particular habitat types was related to human use levels and habitat potential (Paquet et al. 1996). Changes in patterns of habitat use were evident when human activity exceeded 100 people/month. Nearly complete alienation of wolves occurred when >10,000 people/month used an area, regardless of habitat suitability. In portions of the Valley where high elk abundance was associated with high road and/or human population density, wolves were completely absent. Several studies have suggested that ungulate prey seek out predator-free refugia to avoid predation by wolves (Mech 1977c; Holt 1987; Hebblewhite 2000). These changes can lead to different intrinsic rates of growth for ungulates using different habitat patches. Species other than wolves and their prey also may be affected by these human-induced changes in predator–prey relationships.

Use of Den and Rendezvous Sites. Wolves are usually intolerant of humans near dens and pups (Chapman 1977). Researchers, however, have successfully observed den and rendezvous sites without apparent disturbance to the wolves (Joslin 1966, 1967; Theberge 1969; Carbyn 1975a; Mech 1987; 1988). Wolves characteristically respond to human presence near their pups by barking and howling, leaving the area, moving the pups, or deserting the home site (Chapman 1977). Most pups in the presence of humans retreat to the den. Severity of disturbance is the most critical factor influencing desertion of home sites. In only 1 of 51 den site disturbances examined by Chapman (1977) were pups abandoned by the pack. Low-intensity disturbance at den sites seems unlikely to affect the fitness of a wolf population. The seriousness of human disturbance, however, is ultimately a human judgment. Consequently, any alteration of the normal activities of wolves at home sites may be judged by some to be undesirable.

Wolf dens within 1.0 km of established centers of human activity were usually permanently abandoned. Dens within 2.4 km of roads or campgrounds, however, were frequently used by wolves (Chapman 1977). Wolves pups in Banff National Park detected road construction activity from >4 km away and remained in their den until the construction stopped (P. Paquet, unpublished data). Avoidance of human activity seems reduced where artificial sources of food such as garbage dumps are present (Chapman 1977; Paquet et al. 1996; Krizan 1997) or where substantial innocuous human activity occurs. Mortality of pups because of human disturbance has not been reported. Ballard et al. (1987) suggested pup survival is not decreased by den site disturbances. In some areas, wolves may be adapting to human activity and disturbances (Mech 1995). Thiel et al. (1998) reported wolves tolerating human activity near dens and rendezvous sites with pups. These include moss harvesting in Wisconsin and military maneuvers and road construction in Minnesota. In Montana, a pack of wolves kept its pups in a rendezvous site 0.8 km from a helicopter logging operation during summer 1994 (Jimenez 1995).

Chapman (1977) concluded that human disturbance of wolves at levels characteristic of National Parks does not significantly affect survival of wolf pups or seriously alter ecological relationships between wolves and their prey. Denali National Park, Alaska, maintains closures around wolf dens and rendezvous sites, including some rendezvous sites that have not been used in many years. Regulations allowing wolf reintroduction in Yellowstone National Park allow closing areas to human visitation for 1.6 km around active dens from 15 March to 1 July (Fritts et al. 1994). The Wisconsin Department of Natural Resources recommends closing areas within 100 m of dens and restricting use from 100 to 800 m from dens from 1 March to 31 July (A. P. Wydeven, Wisconsin Department of Natural Resources, Park Falls, pers. commun., 2000). Banff National Park, Alberta, protects dens by closing entire watersheds to humans from 1 May to 1 August. Peter Lougheed Provincial Park, Alberta, and Riding Mountain National Park, Manitoba, restrict human activities within 1.6 km of known dens. Based on a comprehensive study of North American Parks, Chapman (1977) recommended a protective buffer around den and rendezvous sites of 2.4 km radius in open country.

Influence of Linear Developments. Ensured connectivity of quality habitats is important for survival of large carnivores (Beier 1993; Doak 1995; Noss et al. 1996), especially for those that face a high risk of mortality from humans or vehicles when traveling across settled landscapes (Noss 1992; Beier 1993). Many human activities associated with linear corridors (highways, secondary roads, railways, power line corridors, gas lines, and seismic lines) fragment wolf ranges and result in the death of wolves (De Vos 1949; Fuller 1989; Paquet et al. 1996; Krizan 1997; Callaghan 2002). Such developments also may be physical and/or psychological impediments to wolf movement (Paquet and Callaghan 1996; Paquet et al. 1996; Duke et al. 2001).

Conversely, linear developments may enhance movements of wolves. Thurber et al. (1994) speculated that roads with low human activity provide easy travel corridors for wolves. Specifically, they serve as conduits or travel corridors for wolves (Paquet et al. 1996; Paquet and Callaghan 1996). The provision of artificial travel corridors, however, should not be construed as a positive development. The overwhelming effects of vehicle collisions and other human-caused mortality factors resulting from increased access, including poaching, hunting, and trapping, outweigh the benefits (Jalkotzy et al. 1997). Moreover, use by wolves of linear corridors increases predation pressure on woodland caribou (James and Stuart-Smith 2000), elk, deer, and coyotes (Paquet 1989).

Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller 1989). Persistent occupancy of wolves is usually assured at mean road densities below 0.6–0.70 km/km^2 (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller 1989; Mech 1989; Fuller et al. 1992; Shelley and Anderson 1995; Boyd-Heger 1997; Frair 1999; but see Merrill 2000).

These thresholds, however, probably do not apply to areas where public access is restricted and activities are regulated (Merrill 2000). To a point, road density may be less important than the mortality of wolves caused by humans using roads. Overall, lethality of a road is a function of frequency of use, traffic speed, and the attitude/motivation of drivers (Merrill 2000). Mech (1989) reported wolves using an area with a road density of 0.76 km/km^2, but it was next to a large, roadless area. He speculated that excessive mortality experienced by wolves in the roaded area was compensated for by individuals that dispersed from the adjacent roadless area. Wolves on Prince of Wales Island, Alaska, used areas with road densities >0.58 km/km^2. Core areas, however, were mostly in the least densely roaded areas of the home range. In addition, wolf activity that does occur in densely roaded areas occurs primarily at night.

A study in Alaska concluded that wolves avoid heavily used roads and areas inhabited by humans, despite low human-caused wolf mortality (Thurber et al. 1994). Landscape level analysis in northern Great Lakes region found mean road density was much lower in pack territories (0.23 km/km^2 in 80% use area) than in random nonpack areas (0.74 km/km^2) or the region overall (0.71 km/km^2). Few areas used by wolves had a road density of >0.45 km/km^2 (Mladenoff et al. 1995). In the Rocky Mountains, wolves killed by humans died closer to roads than wolves that died of other causes (Boyd and Pletscher 1999). However, the relationship of road density and wolf distribution is not well understood in mountainous topography (Singleton 1995; Paquet et al. 1996; Boyd-Heger 1997; Callaghan 2002). In complex mountain terrain, wolves must use valley bottoms, where roads converge with high-quality habitat.

There are several plausible explanations for the absence of wolves in densely roaded areas. Wolves may behaviorally avoid these areas depending on the type of use the road receives (Thurber et al. 1994; Person 2001). In other instances, their absence may be a direct result of higher mortality in areas with greater road density (Van Ballenberghe et al. 1975; Mech 1977a; Berg and Kuehn 1982). Roads and other linear developments provide people access to remote regions, which allows them to deliberately, accidentally, or incidentally kill wolves (Van Ballenberghe et al. 1975; Mech 1977a; Berg and Kuehn 1982; Fuller 1989; Mech 1989). On Prince of Wales Island, Alaska, researchers reported a significant increase in wolf mortality in areas where road density was >0.25 km/km^2 (Person 2001).

RESEARCH NEEDS

The future of wild wolves in an increasingly human-dominated world depends on informed science-based management and decisions (Mech et al. 1997; Theberge et al. 1996). Much of the essential science remains ambiguous however, because most field research is outside the domain of reproducibility and control. Moreover, the impossibility of accounting for unknown processes and variables adds to scientific uncertainty. Wolf researchers, therefore, may need to acknowledge ignorance and emphasize uncovering the limits to reliable knowledge rather than proving existing knowledge to be correct.

In North America, extensive field research on wolf biology and ecology has been carried out in the last 30 years. Information regarding social behavior and physiology of wolves, however, has come largely from captive studies, supplemented by incidental observations in the wild (Haber 1996). Most field studies have emphasized wolf–ungulate interactions primarily as related to humans. Largely overlooked has been the natural role of the wolf as a summit predator (McLaren and Peterson 1994; Terborgh et al. 1999), especially in complex multipredator and multiprey systems. The relationship of wolves with domestic livestock has had only limited scientific inquiry. In addition, a preponderance of quality research from Alaska and the Great Lakes region of the United States and Canada has slanted our understanding of wolves to those environments. Because wolves from the Great Lakes region may be hybrids of gray wolf, red wolf, and coyotes, we should be cautious about generalizing to other regions of North America. Further genetic investigations are needed to more clearly understand the history of hybridization and the implications for gray wolf recovery efforts.

Future research efforts should focus on coexistence of wolves and humans and the ecological processes that sustain them. Because of public interest in the species, refinements in wolf population estimates (Créte and Messier 1987; Fuller and Sampson 1988; Fuller and Snow 1988) and better documentation of numbers of wolves killed annually are required. True sustained-yield management requires more emphasis on qualitative biological features to determine the extent to which wolves and other species with evolutionary histories as predators rather than as prey should be harvested. Research is needed on viability of small wolf populations in human-dominated landscapes, spatial assessments of source–sink populations, and human dimensions of wolf management. The latter should address social issues, economics, traditional knowledge, hunting, trapping, and the potential for aggressive interactions of wolves with humans. More behavioral and ecological research needs to be carried out in agricultural areas, mountainous topography, coastal and island environments, and arid locations such as the southwestern United States and the Arctic. Finally, the role of the wolf in the ecological community needs to be clarified. Specifically, interactions with other carnivores and top-down effects on ungulates and vegetation should be studied. Ironically, the species once regarded as a threat to our survival is turning out to be a test of how likely we are to achieve sustainability and coexistence with the elements that sustain us.

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