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Canis lupus. By L. David Mech

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Canis lupus Linnaeus, 1758

Gray Wolf

Canis lupus Linnaeus, 1758:39. Type locality Sweden.

Canis lycaon Schreber, 1775:pl. 89. Type locality Quebec, by restriction (Goldman, 1937:38).

Lupus Cruzae Sabine, in Franklin, 1823:654, not Griseus Boidaert, 1794.

Canis Lupus-Albus Sabine, in Franklin, 1823:655, not albus Kerr, 1792.


Canis pellipes Sykes, 1831:101. Type locality Deccan, India.

Canis hodophalus Temminck, 1839:284. Type locality India.

Canis variabilis Wied-Neuwied, 1841:95. Type locality Fort Clark, near Stanton, Mercer County, North Dakota.

Lupus orientalis Wagner, 1841:367. Type locality Europe.

Lupus longipennis Hodgson, 1847:474. Type locality "Tibet," but possibly little Tibet in Kashmir.

Canis chanco Gray, 1833:94. Type locality Chinese Tartary.

Canis canis outstandingly larger, with body configuration but distinguishable from them by having almost spherical tympanic bullae as compared with smaller, to 60° in dogs (Iljin, 1941) and having large, convex, and possibly little Tibet in Kashmir.

Canis chango Gray, 1833:94. Type locality Chinese Tartary.

Canis niger Selater, 1874:pl. 78, not niger Kerr, 1792.

Canis pambasileus Elliot, 1905:79. Type locality Susitna River, region of Flin McKinley, Alaska.

Lupus fitchi matsch, 1908:153. Type locality Siningtu, Kansu, China.

Lupus karanorensis Matsch, 1908:159. Type locality Karanor, in the Gobi.

Lupus tschilensianus Matsch, 1908:160. Type locality Coast of Chihli, China.

Lupus alticus Noak, (? ) 1911:465. Type locality Chuluyman, Altai.

Canis tundrarum Miller, 1912:1. Type locality Point Barrow, Alaska.

CUSTOM AND CONTENT. Order Carnivora, Family Canidae. The genus Canis includes eight species. Approximately 24 New World and eight Old World subspecies of C. lupus are recognized, the number depending on authorities accepted. For summary, see Mech (1970); for full synonymy, see Goldman (1937:40). Type locality "Harts Draw, south of Rankin, Upton County, Texas," USA.

C. l. lupus Linnaeus, 1758:39, see above (synonyms are flavus Kerr, niger Hermann, communis Dwigubski, orientalis Wagner, major Ogérian, minor Ogérian, deasul Caberera, signatus Cabrera, lycaon Trouessart, albicus Noak, talicus Altitobelo, and karjik Boklay).

C. l. lycaon Schreber, 1775:pl. 89, see above (synonyms are cunctans Blainville and unguens Comeau).

C. l. albesc Kerr, 1792:137. Type locality Jenisea eastern USSR (synonyms are turcuchensian Ognev, and dybowski Domaniewski).

C. l. orientalis Dwigubski, 1904:10. Type locality between Black Sea and Caspian, Kirghizia, to Yenesei River (synonyms are desertorum Bogdanov, cubansian Ognev).

C. l. nubilus Say, 1823:169, see above (a synonym is variabilis Wied-Neuwied).

C. l. occidentalis Richardson, 1829:60. Type locality Simpson, Mackenzie, Canada (synonyms are stictus Richardson, at Richardson).

C. l. quintana Schreber, 1775:pl. 89, see above.

C. l. hodophalus Temminck, 1839:284, see above (synonyms are hodophalus (sie) Temminck and jenomia Nering).

C. l. maximus Richardson, in Beecher, 1839:5. Type locality Columbia River below the Dalles, between Oregon and Washington, USA (a synonym is gigas Townsend).

C. l. canus Gray, 1833:94, see above (synonyms are langer Hodgson, niger Selater, lichen Maitchi, karmania Matsch, tschilensianus Matsch, and coreanus Abe).

C. l. griscomba Baird, 1858:104. Type locality Cumberland

House, Saskatchewan, Canada (synonyms are Lupus-Griese Sabine, and kniglitis Anderson).

C. l. pambasileus Elliot, 1905:79, see above.

C. l. tundrarum Miller, 1912:1, see above.

C. l. bailey Nelson and Goldman, 1929:165. Type locality Colombia Garcia, Chihuahua, Mexico.

C. l. hattai Kishida, 1939:23. Type locality Sapporo, Hokkaido, Japan (re Pocock is a synonym).

C. l. crassodon Hall, 1932:280. Type locality Tahsis Canal, Nootka Sound, Vancouver Island, B.C., Canada.

C. l. arabs Pocock, 1934:636. Type locality "Ein in S.E. Arabia."

C. l. eion Pocock, 1935:683. Type locality "Cape York, on Baffin Bay, N.W. Greenland."

C. l. arctos Pocock, 1935:682. Type locality "Melville Island, Arctic America."

C. l. beothucus G. M. Allen and Barbour, 1937:230. Type locality "Newfoundland, Canada."

C. l. irremotus Goldman, 1937:41. Type locality "Red Lodge, Carbon County, southwestern Montana."

C. l. labradorius Goldman, 1937:38. Type locality "vicinity of Fort Chimo, Quebec, Canada."

C. l. igoni Goldman, 1937:39. Type locality "head of Duncan Canal, Kuglenuq Island, Alexander Archipelago, Alaska, USA."

C. l. mongololansis Goldman, 1937:43. Type locality "S.A. Creek, 10 miles northwest of Luna, Catron County, New Mexico," USA.

C. l. monstabilis Goldman, 1937:42. Type locality "10 miles south of Rankin, Upton County, Texas," USA.

C. l. youngi Goldman, 1937:40. Type locality "Harts Draw, north slope of Blue Mountains, 20 miles northwest of Monceille, San Juan County, Utah," USA.

C. l. alces Goldman, 1941:109. Type locality Kachemak Bay, Kenai Peninsula, Alaska, USA.

C. l. columbiensis Goldman, 1941:110. Type locality Wistaria, N. side Ootsa Lake, B.C. Canada.

C. l. hodsonius Goldman, 1941:112. Type locality head of Schlute Lake, Keewatin, Canada.

C. l. homards Anderson, 1943:389. Type locality Cape Kellett, SW Banks Island, Franklin, Canada.

C. l. mackenziei Anderson, 1943:390. Type locality Inmanuit, west of Kator Point, Bathurst Inlet, Mackenzie, Canada (a synonym is Lupus-Albus Sabine).

C. l. manningi Anderson, 1943:392. Type locality Hantch River, east Foxe Basin, west side Baffin Island, Franklin, Canada.

DIAGNOSIS AND GENERAL CHARACTERS. Largest member (figure 1) of the Canidae except for certain breeds of domestic dogs (Canis familiaris). Adult females weigh from 18 to 55 kg (40 to 120 lb) and measure 1.37 to 1.52 m (4.5 to 6.0 ft) in total length; and males 20 to 80 kg (45 to 175 lb) and 1.27 to 1.64 m (5.0 to 6.5 ft), depending on subspecies. Far long and varying in color from pure white through noshed gray and brown to coal black; usually grizzled gray. Generally resembling domestic German shepherd or husky in head and body configuration but distinguishable from them by having orbital angle (figure 2) of 40° to 45° as compared with 53° to 60° in dogs (Iljin, 1941) and having large, convex, and almost spherical tympanic bullae as compared with smaller, compressed, and slightly crumpled bullae in dogs. Distinguishable from coyote (Canis latrans) by having larger size, broader snout, relatively shorter ears, and proportionately smaller brain case. Canis raji of eastern Texas and Louisiana is similar to Canis lupus, being intermediate in many characters between wolf and coyote (Nowak, 1970). See "Remarks." Further distinctions among these four closely related and similar animals were detailed by Lawrence and Bessert (1967).

DISTRIBUTION. Formerly throughout Northern Hemisphere south of 20° N latitude (figure 1) in all habitats and topography except deserts and high mountain tops. Deliberate
extermination has restricted present range in North America (see figure 4), and in the Old World to eastern Europe, the Soviet Union, China, and northern India. Remnant populations live in western Europe and Scandinavia.

**FOSSIL RECORD.** A closely related Pleistocene species was found in Cumberland Cave, Maryland (Gidley, 1913).

**FORM.** Guard hairs are 60 to 100 mm long (120 to 150 mm in mane) with imbricate scales that are elongate in proximal region of hair, crenate medially, and flattened distally; underfur has coronal scales (Adorjan and Kolenosky, 1969). Dorsal hairs are generally longer and darker than those of venter; a group of stiff hairs surrounds the precaudal gland on dorsal side of tail about 70 mm from base. Hildebrand (1922) has described details of the integument in the Canidae. Shedding occurs in late spring.

The front foot has five toes, including a short one with a dew claw proximad from other four; the hind foot has four toes. Limb posture is digitigrade; the chest is narrow and keel-like with forelimbs seemingly pressed into chest, and elbows turned inward and paws outward (Young, 1944; Ilijin, 1941). The legs are moderately long. Dentition is 3/3, c 1/1, p 4/4, m 2/3, total 42; canines are about 26 mm long and carnassials are well developed. The cranium is elongate and tapering anteriorly, with long jaws (figure 5). For further details on skull and teeth see Goldman (1944). The baculum is pointed and has a ventral groove. The especially strong and large masticatory muscles allow a powerful bite.

Atkins and Dillon (1971) have compared the brain to that of other canids.

The simple stomach can hold 7 to 9 kg (15 to 20 lb) of food. The liver is relatively large, varying in males from 0.7 to 1.9 kg (1.6 to 4.2 lb) and averaging 1.2 kg (2.6 lb) and in females 0.68 to 0.82 kg (0.5 to 1.8 lb) (Makridin, 1962). Except for minor differences noted in "Diagnosis," anatomy is similar to that of the domestic dog. There normally are 10 mammae (Goldman, 1944).

**FUNCTION.** Fine underfur and long guard hairs conserve a high proportion of body heat, enabling wolves to function in temperatures lower than -40°F. Tireless travel at a usual rate of 8 km per hour and a running gait of 55 to 70 km per hour is facilitated by the animal's long legs and powerful leg muscles (Mech, 1970). The extended rostrum provides abundant surface for the olfactory organ, allowing the wolf to detect odors of prey at distances up to 2.4 km (1.5 mi) under favorable conditions (Mech, 1966). Digestion of food may take place within a few hours (Makridin, 1959). Howling and scent marking via urine posts, feces, and scratching are common and may function in territory maintenance, although direct evidence for this hypothesis is lacking. Growling, with a frequency of 380 to 450 Hz, and barking, at 320 to 904 Hz (Tembreck, 1963), are both at times manifestations of threat. The howling of three adult males was described as follows: "[The howl is] a continuous sound from half a second to 11 seconds in length. It consists of a fundamental frequency which may lie between 150 and 780 cycles per second (Hz), and up to 12 harmonically related overtones. Most of the pitch, the remains constant.
6.5 embryos, and newly maturing females, 6.1 ova and 5.4 embryos (Rausch, 1967). Gestation lasts 63 days, and an average of six young (extremes, one to 11) are born blind and helpless, usually in a hole in the ground, but often in a rock crevice, hollow log, overturned stump, or other place of quiet shelter. The female usually stays near the young for at least 2 months, while the male and other pack members hunt and feed both the female and the pups. Eyes open at day 11 to 15, most milk teeth are present by about week 3, and weaning takes place at about week 5. After about week 8, the pups are moved to a ground nest, where they romp and play over an area of up to an acre (.4 hectare) an area known as a "rendezvous site." The pups may spend up to 3 weeks at one site but are then shifted as far away as 8 km (5 miles) to another. Probably depending on the degree of development of pups, they may continue this behavior even through winter, although pups in good physical condition will join adult members of a pack in their travels as early as October, at which time they may weigh 27 kg (60 lb) and be almost of adult size. Adult teeth replace deciduous teeth between weeks 16 and 26 (Schonberner, 1965). Eruption of the first molar (M1) usually begins at about week 7, and the last premolar (P4) erupts around week 10. Adult teeth are present by about week 3, and weaning takes place at about week 5. After about week 8, the pups are moved to a ground nest, where they romp and play over an area of up to an acre (.4 hectare) an area known as a "rendezvous site." The pups may spend up to 3 weeks at one site but are then shifted as far away as 8 km (5 miles) to another. Probably depending on the degree of development of pups, they may continue this behavior even through winter, although pups in good physical condition will join adult members of a pack in their travels as early as October, at which time they may weigh 27 kg (60 lb) and be almost of adult size. Adult teeth replace deciduous teeth between weeks 16 and 26 (Schonberner, 1965). Eruption of the first molar (M1) usually begins at about week 7, and the last premolar (P4) erupts around week 10. The pups may spend up to 3 weeks at one site but are then shifted as far away as 8 km (5 miles) to another. Probably depending on the degree of development of pups, they may continue this behavior even through winter, although pups in good physical condition will join adult members of a pack in their travels as early as October, at which time they may weigh 27 kg (60 lb) and be almost of adult size. Adult teeth replace deciduous teeth between weeks 16 and 26 (Schonberner, 1965).
moose per wolf per 45 days (Mech, 1966), with corresponding average estimated consumption rates being 2.5 kg (5.6 lb) of deer per wolf per day to 6.3 kg (13.9 lb) of moose per wolf per day. Remains of kills often supply food to such scavengers as ravens (Corvus corax), bald eagles (Haliaeetus leucocephalus), foxes (Vulpes), and other small birds and mammals. Ravens frequently follow wolf packs for miles, evidently in search of such food.

According to Mech (1970) who summarized the reports of parasites in wolves, the following have been recorded: nine species of flukes (Trematoda), 21 species of tapeworms (Cestoda), 24 species of roundworms (Nematoda), three species of spiny-headed worms (Acanthocephala), two species of lice, one species of flies, seven species of ticks, one species of tongue worm, and one species of mange mite. Probably the most important parasite of the wolf is Echinococcus granulosus, the hydatid tapeworm, the larval stage of which can infect man. Diseases known for the wolf include rabies, distemper, arthritis, cancer, and miscellaneous other disorders (Mech, 1970).

Few animals compete successfully with the wolf, except for man and perhaps the cougar (Felisconcolor). There is some evidence (Mech, 1970) that high densities of wolves may reduce populations of the coyote (Canis latrans), wolverine (Gulo gulo), and lynx (Lynx canadensis).

The age structure of wolves in an unexploited population in Ontario was 35% pups, 40% yearlings, and 25% adults (Pimlott et al., 1969), whereas in an exploited population in Alaska it was 42% pups, 29% yearlings, and 29% adults (Rausch, 1967). Mech (1970) has calculated that survival rates of wolves in unexploited populations are 6 to 43% for pups from birth to first winter, 55% from first to second winter, and about 80% annually for adults. Mortality factors include diseases, parasites, starvation, intra-specific strife, injuries by prey, and exploitation and persecution by man and bears.

Wolves travel a great deal, usually more at night but often during the day if the temperature is cool (Mech, 1970). Three types of movements can be distinguished—(1) travels within home range, (2) dispersal, and (3) migrations. Home range varies from 130 km² (50 mi²) in Minnesota (Mech and Frenzel, 1971) to 13,000 km² (5000 mi²) in Alaska (Berkholder, 1959). Daily travels within home range vary from a few kilometers per day to up to 145 miles. A dispersing wolf traveled a straight-line distance of 206 km (128 mi) in 2 months (Mech and Frenzel, 1971). In tundra areas, wolves follow migrating caribou herds and thus annually travel more than 100 km (100 mi), one way, from tundra to taiga and back (Kelsall, 1968). The farthest individual migrating wolf traveled is 360 km (225 mi) (Kutz, 1972).

Studies in progress in Minnesota (Mech, unpublished) show that family groups or packs occupy exclusive home ranges, and that lone wolves cover much larger areas, shifting about amongst these, and being chased by the resident packs. Highest known natural density of wolf populations anywhere on a year-around basis is one wolf per 26 km² (10 mi²) on the average (Pimlott, 1967).

Few other species have had such a diversity of relationships with man as has the wolf. Evidently early humans tamed wolves and domesticated them, eventually selectively breeding them and finally developing the domestic dog (Canis familiaris) from them. At present, the taming of wolves for pets continues, a process not difficult if considerable time is devoted to it, and wolf farms now sell pups for $100 to $350 each. Most of these animals end up in zoos. Because of the wolf’s habit of killing domestic livestock, the species was exterminated by bounty, poisoning, and government control programs in more than 80% of the area of the 48 contiguous United States, in much of Mexico, in the settled farming areas of Canada, in most of western Europe, and in much of eastern Europe and the Soviet Union. In the latter two areas, concerted programs of extermination continue (Fuller, 1965), although there is some evidence that official policy toward the wolf in the USSR is changing (Oshman, 1971). Various Indian provinces still pay bounties on wolves, although in most of these areas little damage to livestock is done. The wolf is informally considered in danger of extinction in Mexico. In the United States outside of Alaska, six of the eight subspecies that originally occurred at least in part in the country are now considered extinct there, (C. T. occidentalis and C. I. irremutus are officially on the Secretary of the Interior’s list of endangered animals). The possibility of the occurrence of some C. I. nubilus in Minnesota has been raised by Mech and Frenzel (1971). In Alaska, there are restrictions on taking wolves in some areas, and bounties on them are legally protected by state laws (Harper, 1970). Wolves are legally protected in Michigan, where a small remnant population exists, in Wisconsin, where there may be a few individuals, and in Isle Royale National Park, where the population numbers 20 to 30 (Mech, 1966; Jordan et al., 1967). In the Superior National Forest of Minnesota, wolves are protected by federal law, although state laws allow almost unrestricted taking, and in some parts of Minnesota state control programs offering $50 per animal killed are in effect. Several hundred wolves are still present in the state, with an estimated 300 to 400 living in Superior National Forest (Mech, 1973).

Wolf fur is used for parkas, mukluks, and rugs. Raw wolf pelts from forested areas sell for $15 to $100 depending on quality and color. Arctic wolves bring higher prices than those from other regions. Wolves are hunted for sport in parts of Alaska and Canada, usually with an aircraft searching for the animals on frozen lakes or open tundra. Trapping wolves for fur and bounty remains lucrative for some Indians, Eskimos, and a few whites.

The main methods of studying wolves have been natural observation in open areas, aerial tracking and observation in winter, live-trapping via steel traps and snares with locks, and tagging with radio-collars. For anesthetizing wild-caught wolves, a combined intramuscular injection of 30 mg of phencyclidine hydrochloride and 25 mg of promazine hydrochloride has been successful (Neal and Erickson, 1966; Jordan and others, 1967). Prevention by legal hunting is of importance. Controlling the occurrence of some C. I. nubilus in Minnesota has been raised by Mech and Frenzel (1971). In Alaska, there are restrictions on taking wolves in some areas, and bounties on them are legally protected by state laws (Harper, 1970). Wolves are legally protected in Michigan, where a small remnant population exists, in Wisconsin, where there may be a few individuals, and in Isle Royale National Park, where the population numbers 20 to 30 (Mech, 1966; Jordan et al., 1967). In the Superior National Forest of Minnesota, wolves are protected by federal law, although state laws allow almost unrestricted taking, and in some parts of Minnesota state control programs offering $50 per animal killed are in effect. Several hundred wolves are still present in the state, with an estimated 300 to 400 living in Superior National Forest (Mech, 1973).

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BEHAVIOR. The wolf is a social animal, usually functioning in packs that are basically family groups (Mech, 1970). Packs usually contain 5 to 8 members, but packs of up to 36 have been reported (Rausch, 1967). Packs are held together by means of affectional ties that develop, are reciprocated, and become fixed in packs during the first 5 months of life, or by courtship behavior between two lone mature adults. Order is maintained in the pack by a dominance hierarchy with the adult male dominant to the adult female and pups, the female dominant to the pups, and a linear order among the pups. In larger packs a male order and female order develops among adults, but the leader is almost always a male, known as the "alpha male." In most interactions between two wolves, one greets the other by demonstrating its dominance, while the other indicates submission (Schenkel, 1947). The dominant posture includes a stiff-legged stance, ears erect and forward, lips pulled forward, mean snarling, and tail vertical. The teeth may be bared, and there may be growling. There are two types of submission, active and passive. Active submission is less intense and involves drawing back of the lips and ears, rapid thrusting out of the tongue, lowering of the hind quarters, and pulling of the tail alongside or between the legs. The entire body is usually lowered and the muzzle is pointed upward toward the mouth of the dominant animal and may touch it. This is often accompanied by whining and urinating. In passive submission, which commonly occurs when a wolf rolls onto its back and in its paws toward its body, and often urinates. According to Schenkel (1967), this behavior develops from the elimination posture of young pups in which the adult licks the perineal area, stimulating and ingesting the waste of the pup. Active submission may be induced by a food-begging posture in pups, causing the adults to regurgitate food to them, the usual method of weaning and feeding of pups for the first several months of their life. Social rank in pups is probably established normally through play-fighting, but when two pups raised by Mech (1970), apart from their parents, fought seriously at the age of 30 days, established their relative ranks at that time, and never fought after that. Social interactions and dominance demonstrations occur every day throughout the year in Intermountain wolves. At that time some contests in rank may take place, but these only occur among adult members. Only rarely is intrapack fighting reported to occur.

Courtship between previously unmated wolves may take place several months before breeding (Craiter, 1958) or just a few days before the breeding season (Mech, unpublished). Courtship consists of a great deal of sniffing, nipping, head rubbing, snout grabbing, tail wagging, and general play with contact. Either male or female may assume a paw or neck across the back of the other. The female, when receptive, will lift her tail and display her vulva. Mounting may take place from the side initially but is soon oriented from behind, with the male grasping the female around the chest and neck, and thrusting until the buttocks of his penis is locked behind the vaginal sphincter. While the pair is still locked together by their genitals the male dismounts, lifts a hind leg over his partner's back and turns his body 180° away from her. The pair then remain coupled, back to back, for as long as 30 minutes, during which ejaculation occurs many times.

There are three main methods of communication among wolves: (1) howling and other vocalizations; (2) visual display including postures and positions of various body parts especially the face; and (3) scent-marking. It is known that individual wolves may have distinctive howls (Theberge and Fults, 1967). The howling of pups is usually high-pitched, with crashing, whereas the pitch of adults is much lower. One of the functions of howling is in assembling the pack, and territory advertisement is suspected as another. Coarse barking, whining, and growling are other vocalizations. Body positions and facial expressions show social status primarily, as described above. Inginal presentation and sniffing are also involved in status demonstrations, but probably also serve in individual identification. Scent-marking (Kleiman, 1966) involves deposition of urine and/or feces on conspicuous objects, trails, and often delinquent areas of the earth. It is usually performed by high-ranking adult males, often at trail intersections (Mech and Frenzel, 1971). It is speculated that scent-marking is a means of advertising territory that has not been proven. Wolves are good swimmers and do not hesitate to wade or swim across rivers and lakes; they sometimes follow prey into water even in winter (Pimlott et al., 1969). Wolves rest on their sides usually, although they sometimes rest on their abdomen; when sleeping deeply, they lie curled up nose beneath tail. Play involves chasing, ambushing, and mock fighting, and these activities may help each pup determine its social status among its peers. Behavior of wolves has been altered by trapping and castrating pups (Schenkel, 1947; Rabh et al., 1967), by long-range observation (Muir, 1944), and through the use of aircraft in winter (Mech, 1966; Jordan et al., 1967; Hader, 1973). Extensive studies comparing the behavior of wolves in captivity with that of other canids are being conducted by Fox (1972).

GENETICS. To date no differences in karyotypes have been found between the wolf and the domestic dog or the coyote (Hungerford and Snyder, 1966), or the red wolf (Nowak, 1970). According to Hsu and Benirschke (1967), both dog and coyote have 39 pairs of chromosomes, with the autosomes described as "acrocentrics or telocentrics" and the sex chromosomes as "submetacentric" for the X and "minute" for the Y in the coyote and "minute metacentric" for the Y in the dog. Hjinn (1941) crossed a wolf with a black mongrel sheep dog and then made various types of crosses for four generations, totaling 101 individuals, all of which were fertile.

REMARKS. Jolicoeur (1959) concluded that there are probably far too many subspecies of Canis lupus recognized, and the author concurs. Some of the subspecies have been described on the basis of only a few specimens. The relationship between Canis lupus and the red wolf (C. rufus) is unclear, but Lawrence and Bostert (1967) presented evidence that C. rufus may be a hybrid between lupus and latrans. Paradiso (1968), Nowak (1970), and Atkins and Dillon (1971) treat rufus as a distinct species.

Goldman (1944) summarized the taxonomy of the wolves of North America, and Young (1944) presented considerable historical information about the species. Rutter and Pimlott (1968) condensed much of the ecological and behavioral material on the wolf for popular consumption, and Mech (1970) synthesized most of the technical information that was available about the animal through 1968. Fox (1972) detailed the behavior of wolves in comparisons with other canids.

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LITERATURE CITED


