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Gulo gulo.

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Gulo Pallas, 1780

Gulo Pallas, 1780:25. Type species *Gulo sibiricus* Pallas [=*Mustela gulo* Linnaeus]

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae. Some authors (Anthony, 1928; Miller, 1912; Miller and Kellogg, 1955; Ognev, 1935) place the wolverine into its own subfamily, Guloninae, while others (Ellerman and Morrison-Scott, 1966; Stroganov, 1969; Wilson and Reeder, 1993) include it in the subfamily Mustelinae. Wilson and Reeder (1993) recognize one living species.

Gulo gulo Linnaeus, 1758

Wolverine

[*Mustela*] *gulo* Linnaeus, 1758:45. Type locality "Sweden, Lapland."
[*Ursus*] *luscus* Linnaeus, 1758:47. Type locality "Hudson Bay."
Gulo sibiricus Pallas, 1780:25. Renaming of *Ursus gulo.*
Gulo borealis Nilsson, 1820:95. Renaming of *Mustela gulo.*
Gulo arcticus Desmarest, 1820:174. Renaming of *Mustela gulo.*
Gulo arctos Kaup, 1829:68. Renaming of *Mustela gulo.*
Gulo luteus Elliot, 1904:260. Type locality "Mount Whitney, Tulare County, California."
Gulo hylaeus Elliot, 1905:81. Type locality "Susitna River, region of Mount McKinley, Alaska."
Gulo biedermanni Matschie, 1918:147. Type locality "mountains south of Lake Teletzkoie, Siberian Altai."
Gulo wachei Matschie, 1918:147. Type locality "north of Beluha Mountains, in upper reaches of River Katun, Siberian Altai."
Gulo niediecki Matschie, 1918:148. Type locality "Dease Lake, British Columbia, Canada."
Gulo katschemakensis Matschie, 1918:151. Type locality "Katschemak Bay, Kenai Peninsula, Alaska."
Gulo auduboni Matschie, 1918:153. Type locality "Newfoundland and Rensselaer County, New York."
Gulo bairdi Matschie, 1918:153. Type locality "Fort Union, near present town of Buford, Williams County, North Dakota."

CONTEXT AND CONTENT. Context is noted in the generic summary above. *Gulo* is monotypic if the Palaearctic and Nearctic forms are considered conspecific. The taxonomic relationship between wolverines from North America and Eurasia has been long debated. Some authorities separate the wolverine into two species, *Gulo gulo* and *Gulo luscus* (Cowan, 1930; Hall, 1981; Miller, 1912); others (Degerbøl and Freuchen, 1935; Ellerman and Morrison-Scott, 1966; Kurtén and Rausch, 1959; Rausch, 1953) consider the Old and New World wolverines to comprise two subspecies, *Gulo gulo gulo* and *Gulo gulo luscus.* Currently, the genus *Gulo* is considered to have only one extant species, *Gulo gulo* (Bryant, 1987; Nowak and Paradiso, 1983; Wilson and Reeder, 1993).

G. g. albus Kerr, 1792:190. Type locality "Kamchatka."
G. g. gulo Linnaeus, 1758:45, see above (*sibiricus, borealis, arcticus, arctos, biedermanni,* and *wachei* are synonyms).
G. g. katschemakensis Matschie, 1918:151, see above.
G. g. luscus Linnaeus, 1758:47, see above (*hylaeus, niediecki, auduboni,* and *bairdi* are synonyms).
G. g. luteus Elliot, 1904:260, see above.
G. g. vancouverensis Goldman, 1935:177. Type locality "Great Central Lake, Vancouver Island, British Columbia."

DIAGNOSIS. *Gulo gulo* (Fig. 1) is the largest extant terrestrial North American member of the family Mustelidae (Allen, 1972; Hall, 1981). Body morphology and proportions of the wolverine are somewhat bear-like, and it is the heaviest and most powerfully built of all terrestrial mustelids (Ewer, 1973; Forsyth, 1985; Jackson, 1961; Nowak and Paradiso, 1983). The wolverine is distinguished from other Mustelinae by its large size and peculiarities in skull and dental structure (Stroganov, 1969). In comparison to other mustelids, the skull of the wolverine is extremely robust and broad, measuring >85 mm in width (Banfield, 1987; Hash, 1987; Peterson, 1966; Wilson, 1982). Zygomatic arches are extraordinarily ponderous, and the sagittal crest is very well developed. Being a scavenger, the ability to crush bones and feed on frozen carcasses is essential to the wolverine's survival (Wiig, 1989). The mandibular and dental structures are extremely strong and capable of crushing almost all the larger bones of adult ungulates (Douglas and Strickland, 1987; Hash, 1987; Stroganov, 1969). In contrast to most members of the genus *Mustela,* which have three premolars in the upper and lower jaw, wolverines possess four upper and lower premolars (Hall, 1981). Although martens and fishers (*Martes* sp.) have the same dental formula as wolverines, the wolverine's teeth are considerably larger, wider, and heavier, and the carnassial teeth are especially well-suited for shearing (Hash, 1987; Jackson, 1961; Shufeldt, 1924).

GENERAL CHARACTERS. The wolverine is often described either as resembling a giant marten (Ewer, 1973; Nowak and Paradiso, 1983; Stroganov, 1969) or a small bear (*Ursus* sp.) (Jackson, 1961; Macdonald, 1985; Peterson, 1966). The species is characterized by a large head, broad forehead, short stout neck, relatively short legs, compact thick skeletal structures, arched back, and heavy musculature. The head and tail are carried lower than the arched back. The feet are large with powerful semiretractile claws, and hindfeet are slightly smaller than the forefeet. Wolverines have short, round, well-furred ears, small, beady eyes, and a bushy tail that is about one-fifth of total length (Hash, 1987; Jackson, 1961; Stroganov, 1969; Wilson, 1982; Wooding, 1982). Coat color varies from medium brown to black. Generally, the head, saddle, tail, and legs are darker than the facial mask and upper body stripe. The stripe may be creamy, pale yellow, light brown, or reddish and extends from the head and shoulders to the back and joins across the base of the tail. Light or white patches on the throat and chest are also common. Occasionally, cream-colored animals with brownish feet have been trapped (Hash, 1987; Stroganov, 1969).

Total body length of adults varies from 900 to 1,125 mm (Hall, 1981) and height at the shoulder is approximately 355–432 mm (Walker, 1975). Mass is usually 10.9–18.1 kg (Hall, 1981)

FIG. 1. Adult female *Gulo gulo.* (Photograph courtesy of Steve Kroschel, Kroschel Films, MN).

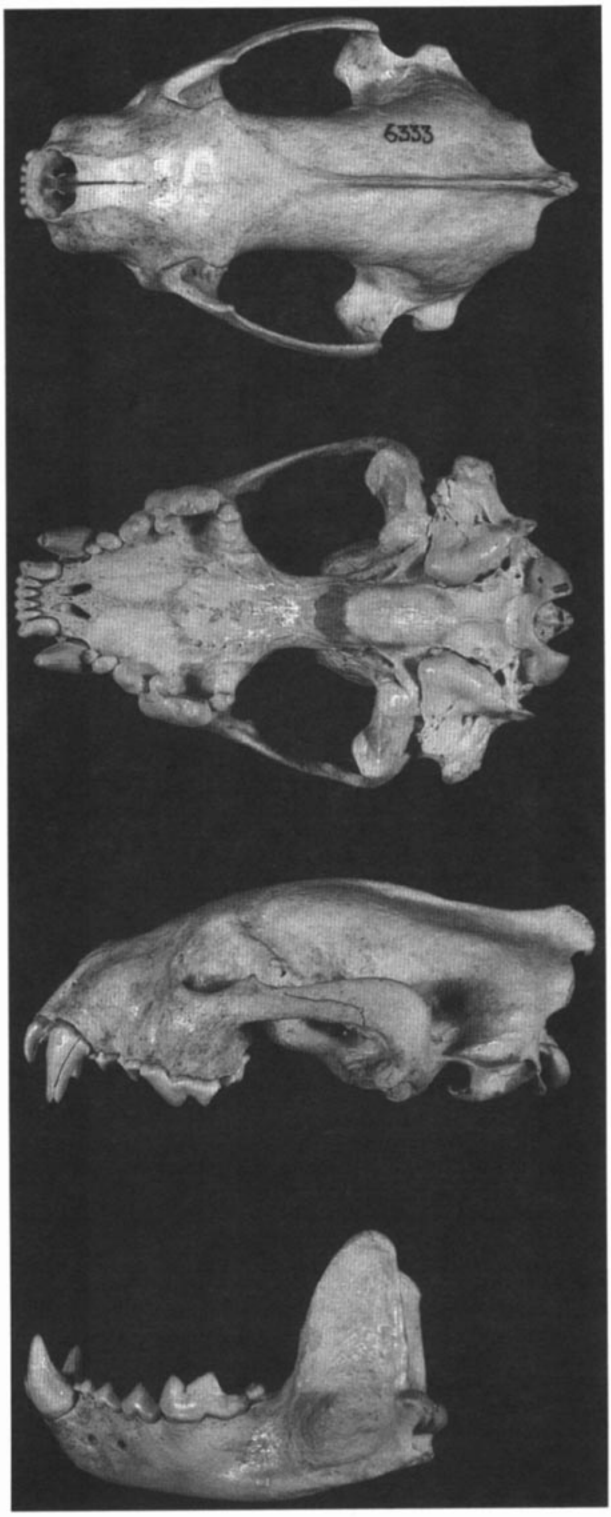

FIG. 2. Skull of *Gulo gulo* (Museum of Natural History, Regina, 6333, male, trapped April 1953, locality unknown). Greatest length of cranium is 133.7 mm.

but may be as much as 32.0 kg (Nowak and Paradiso, 1983). The species is sexually dimorphic. On average, males are 10% larger in linear measurements and 30% heavier in mass than females (Hall, 1981). Mean body measurements and ranges (mm) of adult males and females, respectively, are: total length, 1,000 (940–1,070), 901 (865–932); length of tail, 231 (218–260), 223 (210–250); length of hindfoot, 184 (178–190), 160 (155–165). Mass (kg) of males and females is 14.8 (11.3–16.2) and 10.6 (6.6–14.8) kg, respectively (Banfield, 1987). Body measurements (mm) and mass (g) of 1-day-old kits born in captivity (two males and one female, respectively), are: length of body, 157.5, 157.0; length of tail, 28.9, 26.0; length of foot, 23.7, 23.0; length of ear, 4.9, 5.1; and mass, 85.1, 94.1 (Shilo and Tamarovskaya, 1981).

Skulls of wolverines are massive and heavy (Fig. 2), indicative of a mammal possessing great jaw strength and capable of inflicting a tremendous bite (Shufeldt, 1924). Sexual dimorphism and some geographic variation in skull morphology are also apparent. Geographic variation among populations likely results from interactions of different genotypes and dissimilar environmental conditions (Wiig, 1989). In northeastern Siberia and Kamchatka, average cranial measurements (mm) of male and female wolverines ($n = 12$), respectively, are: condylobasal length, 155.0, 146.0; zygomatic width, 105.0, 99.0; interorbital width, 43.0, 41.2; postorbital width, 33.7, 32.6; mastoid width, 90.6, 86.0; length of upper toothrow, 57.2, 55.3 (Stroganov, 1969). Average cranial measurements (mm) of male ($n = 97$) and female ($n = 77$) Norwegian wolverines, respectively, are: condylobasal length, 152.2, 139.4; palatal length, 80.3, 73.4; rostrum breadth, 41.4, 36.9; zygomatic breadth, 106.1, 94.3; interorbital constriction, 41.0, 37.6; postorbital constriction, 33.9, 32.0; mastoid breadth, 89.3, 80.2 (Wiig, 1989). In comparison, average cranial measurements (mm) of male ($n = 27$) and female ($n = 10$) Alaskan wolverines, respectively, are: condylobasal length, 145.0, 134.6; zygomatic width, 104.6, 95.3; squamosal constriction, 78.5, 71.0; interorbital width, 41.0, 37.9; palatal length, 75.2, 69.4; maxillary tooth row length, 53.4, 50.0 (Rausch, 1953).

DISTRIBUTION. The wolverine has a circumpolar distribution that corresponds with the boreal zone of the northern hemisphere (Kvam et al., 1988; Fig. 3). It is found throughout the holarctic taiga and forest tundra of higher latitudes, south to 37°N in North America and 50°N in Eurasia (Wilson and Reeder, 1993).

Historically, North American wolverines were distributed throughout the northern part of the continent including Alaska, most of Canada, the northern tier of states in the continental U.S.A., and south along the Rocky Mountains to Arizona and New Mexico (Hash, 1987). Current distribution and numbers of wolverines in North America have been notably reduced. By the 20th century the wolverine was extirpated from most of the contiguous U.S.A. (Nowak and Paradiso, 1983). Widespread and viable wolverine populations occur primarily in Alaska and the Rocky Mountains of Montana. Wolverines were apparently near extirpation in most areas of Montana by 1920, but the population has reestablished itself through dispersal from Canada and Glacier National Park (Newby and McDougal, 1964; Newby and Wright, 1955). In California (Kovach, 1981; Yocom, 1973), Washington (Johnson, 1977; Yocom, 1973), Oregon (Yocom, 1973), Idaho (Groves, 1988; Pengelly, 1951), and Wyoming (Hoak et al., 1982) wolverines were never abundant. In Colorado, wolverines remain rare (Nead et al., 1985). From current records, it is highly unlikely that wolverines exist in the remaining states of the U.S.A. (Wilson, 1982). Early records from Indiana, Iowa, Minnesota, Nebraska, Nevada, New Hampshire, New York, Ohio, Pennsylvania, South Dakota, Vermont, Utah, Wisconsin, and Wyoming indicate that wolverines probably did occur in these states at one time. There are no recent records of wolverines in Maine and only unverified early reports. Similarly, there apparently are no confirmed records of wolverines in Michigan, New Mexico, and North Dakota, so it is uncertain whether wolverines ever occurred in these states (Wilson, 1982).

In Canada, wolverines are sparsely distributed in boreal forests from east to west, and inhabit the Arctic archipelago as far north as Ellesmere Island (Banfield, 1987). Until the turn of the century, wolverines inhabited much of eastern Canada except for Prince Edward Island, Nova Scotia, Newfoundland, eastern New Brunswick, Gaspé Peninsula, and Anticosti Island (Banfield, 1987; Peterson, 1966). Presently, the wolverine is extremely rare in Quebec and Ontario, and there are no recent records from Labrador (Prescott, 1983; van Zyll de Jong, 1975). In Manitoba and Saskatchewan, numbers appear to have declined, the southern limits have receded to the north, and wolverines are now confined to the northern portions of the provinces (van Zyll de Jong, 1975). In Alberta, the species once occurred in all coniferous forests of the province, but now is found only in remote areas in the north and in the Rocky Mountains of Alberta (Soper, 1964). The distribution of the wolverine has remained relatively unchanged in British Columbia, Yukon, and Northwest Territories. The Yukon and mainland Northwest Territories support the most extensive and viable populations in Canada.

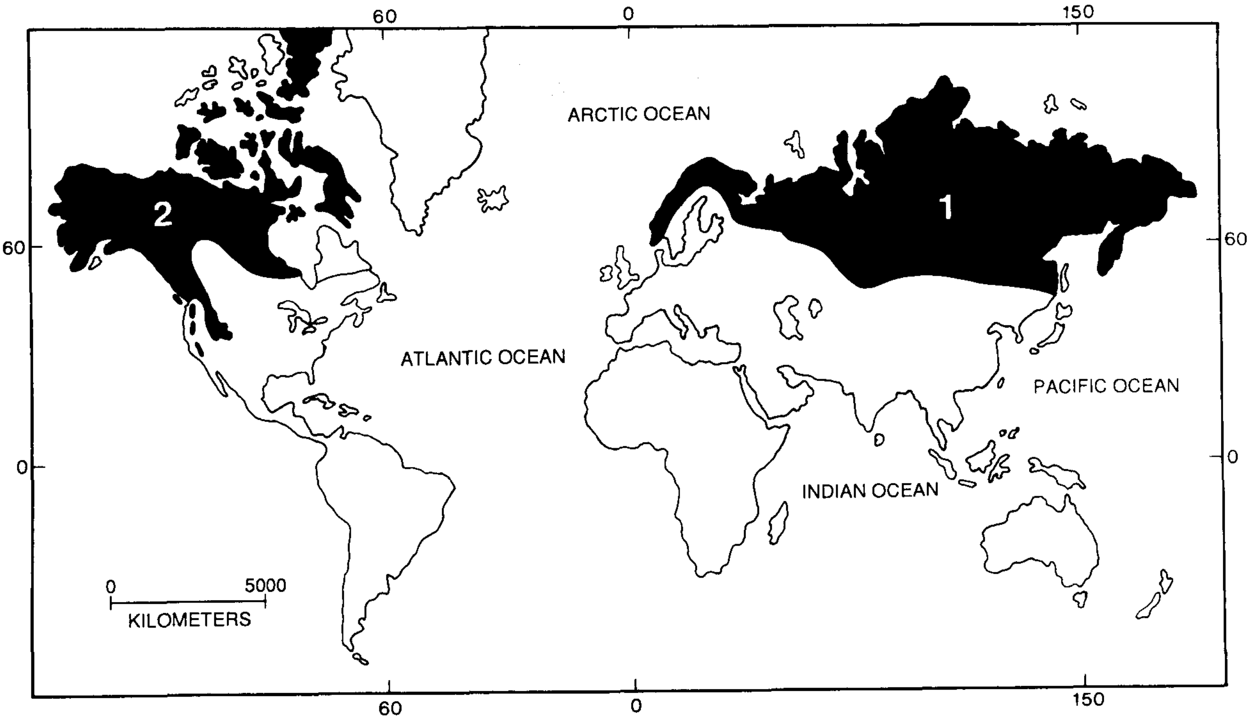

FIG. 3. Geographic distribution of *Gulo gulo* in Eurasia and North America: the two subspecies from the Old and New World are (1) *G. g. gulo* and (2) *G. g. luscus,* respectively. (Sources: Banfield, 1987; Hash, 1987; Kvam et al., 1988; Peterson, 1966; van Zyll de Jong, 1975; Wilson, 1982).

Small numbers of wolverines also inhabit the islands of Banks, Victoria, Melville, Baffin, Ellesmere, and Little Cornwallis (van Zyll de Jong, 1975).

In Eurasia, wolverines are found from Scandinavia eastward through eastern Europe, Siberia, and Asia (Ewer, 1973; Makridin, 1964; Stroganov, 1969; Wilson and Reeder, 1993). Records from Scandinavia show that wolverines occur in low population densities (Nowak and Paradiso, 1983). Most animals are concentrated in the mountain chain of northern Norway and Sweden, and along the south-central Norwegian mountains. In Sweden, wolverines are restricted to remote areas in the northwest. The numbers appear to be increasing; however, the distribution is very irregular (Bjärvall, 1982). Their distribution is correlated with that of wild and semidomestic reindeer (*Rangifer tarandus*), which are their most important food (Bjärvall, 1982; Haglund, 1966; Kvam et al., 1988). In 1986, a maximum of 40 wolverines was recorded in Finland, and the species is now considered endangered (Pulliainen, 1988). Wolverines are also found in the tundra and forest zones of eastern Europe, Russia, and northern Asia. In western Siberia, wolverines are widely distributed in the tundra and taiga, and are relatively common in extreme eastern Russia (Stroganov, 1969).

FOSSIL RECORD. The fossil history of the Mustelidae has not been well documented because most members were small and forest-dwelling. The earliest known mustelids were from late Eocene deposits, and a few marten-like animals were found in the Oligocene (Kurtén and Anderson, 1980). Towards the end of the Miocene, recognizable martens were present. Quaternary mustelids survived in nearly all habitats from the Arctic tundra to tropical rainforests (Kurtén and Anderson, 1980).

The largest of the Mustelinae, *Gulo*, is a holarctic genus specialized for feeding on larger vertebrate prey. The wolverine has no exact counterpart in the tropics (Eisenberg, 1981). *Gulo* is descended from *Plesiogulo*, a large Miocene and Pliocene form (Kurtén and Anderson, 1980). The genus *Plesiogulo* originated in Asia and migrated to North America between 7.0 and 6.5 million years ago (Harrison, 1981). *Plesiogulo* was apparently derived from marten-like ancestors originating from an early Miocene member of the genus *Martes* (Kurtén, 1968).

Advanced forms of *Plesiogulo* show definite progress towards the *Gulo* stage; the transition to the modern genus most likely took place in the Villafranchian (Kurtén, 1968). American and European records of *Gulo* are approximately contemporaneous, but the American may possibly be older. Port Kennedy Cave is the oldest North American fauna that includes *Gulo*, and its estimated age ranges from Yarmouthian to Aftonian (Bryant, 1987). The Aftonian age predates the earliest European record of *Gulo* from the Waalian inter-glacial (Bryant, 1987; Kurtén and Anderson, 1980). *Gulo gulo* is descended from *Gulo schlosseri,* which is smaller than *G. gulo* and shows differences in dental morphology (Kurtén and Anderson, 1980). The transition between the two is gradual and suggests that *G. schlosseri* was the direct ancestor of *G. gulo* (Kurtén, 1968).

Rare fossil remains (fragments of upper and lower jaws and isolated teeth) of *G. gulo* were discovered from Tornewton Cave, South Devon, and are dated from the intermediate epoch between early Cromerian deposits and the Last Glaciation (Kurtén, 1973). In dental allometry patterns, *G. gulo* from Tornewton Cave is similar to the late Pleistocene forms of Europe; however, the late Pleistocene forms are significantly larger than the Tornewton Cave specimens (Kurtén, 1973). Wolverines are also rare in Pleistocene deposits (Anderson, 1977; Kurtén and Anderson, 1980) and are exemplified by remains discovered in Stump Cross Cave in northern England (Sutcliffe et al., 1985). After its appearance in Irvingtonian, *Gulo* is not recorded until Wisconsinan (Kurtén and Anderson, 1980). Some Wisconsinan animals were particularly large; one skull from Fairbanks had a condylobasal length of 172 mm (Kurtén and Anderson, 1980). In comparison, more recent samples from Alaska have a condylobasal length of 130–150 mm (Anderson, 1977).

Wolverines from the Old and New Worlds were formerly considered to be separate species (Cowan, 1930; Hall, 1981; Miller, 1912); however, Kurtén and Rausch (1959) found the two populations to be only subspecifically distinct. Bryant (1987) examined *Gulo gulo* from Pleistocene and concluded that any division of *Gulo* into two species was arbitrary. Studies of Quaternary remains indicate evolutionary progression within a single species, with differences among populations not being substantial enough to warrant separation into two distinct species (Bryant, 1987).

FORM AND FUNCTION. The pelage of the wolverine consists of dense and woolly underfur 2–3 cm in length and coarse guard hairs approximately 6–10 cm long. In winter, the dense underfur forms a thick cushion and the guard hairs are abundant and long. Summer fur is shorter, coarser, and less glossy than winter fur (Stroganov, 1969). Fur is thick but short on the head and becomes progressively longer towards the posterior of the body (Hash, 1987). The tail is shaggy with long guard hairs measuring 15–20 cm (Wilson, 1982).

The Mustelinae typically exhibit reduced dentition and are highly specialized as carnivores (Eisenberg, 1981). The dental formula of the wolverine is i 3/3, c 1/1, p 4/4, m 1/2, for a total of 38 teeth (Peterson, 1966). The jaws and teeth are extremely strong and capable of crushing bones of large ungulates such as deer (*Odocoileus* sp.), caribou, and moose (*Alces alces*; Banfield, 1987; Sutcliffe et al., 1985). The canid-like jaws have a bone-crushing bite similar to that of a spotted hyena (*Crocuta crocuta*; Banfield, 1987; Forsyth, 1985). The upper molar is displaced medially from the toothrow, and the upper carnassial tooth is extremely large. The third upper incisor is larger than the others and like that of the brown bear (*Ursus arctos*). Upper canines are broad at the base and blunt, while the lower canines are short and curved. The middle two incisors of the lower jaw are displaced posteriorly from the other pairs, and this displacement apparently increases strength without the need for more space (Stroganov, 1969; Wilson, 1982). The mean upper tooth measurements (mm, range in parentheses) of male wolverines ($n = 18$) from northern Alaska are: length (anterior to posterior) of canine, 11.1 (10.4–12.2), length (anterior to posterior) of carnassial 21.2 (20.2–21.9), transverse diameter of molar 14.0 (13.4–15.0; Newby and Wright, 1955). Associated with the strong teeth are powerful jaw and neck muscles. The sagittal crest protrudes above the top of the skull and far past the back of the head to provide a large area of attachment for the well-developed temporalis muscles (Kurtén and Anderson, 1980; Stroganov, 1969).

Gulo have a short growth period. Wolverine kits, which are born in February or March, reach adult size in October. Iversen (1972) found that during the wolverine's first 2.5 months of life the basal metabolic rate increased in proportion to the 1.41 power of body weight ($W^{1.41}$). In contrast, heat production in many other mammals increases proportionally to simple body weight ($W^{1.0}$). This increase in total heat production recorded during the early growth phase in wolverines may be attributed to the faster growth of high energy producing tissues such as brain, heart, liver and kidney. After attainment of 2.5 months of age and a mass of 3 kg, a "metabolic break" in heat production was observed. In wolverines, as in other mammals, the "metabolic break" coincided with time of weaning and may reflect a change in food composition or change in activity and thermoregulation of the litter when the mother is absent for longer periods. After termination of growth the metabolic rate per unit of body weight continued to decrease. This decrease is seen in most mammals and is indicative of the slowng of life processes in aging tissues (Iversen, 1972).

Many skull characteristics of wolverines exhibit rapid postnatal growth, and by 9 months of age both sexes show a stabilization in growth. Some skull characteristics, such as width of interorbital constriction, zygomatic breadth, and condyle breadth continue to grow in animals older than one year (Wiig, 1989). The post-cranial skeleton of the wolverine also develops quickly for an animal of its size, and long-bone epiphyseal junctions are apparently closed by 9–10 months of age. The skeletal structure of the adult animal supports a heavy, stout, and muscular body (Banfield, 1987; Rausch and Pearson, 1972).

The gross mass, mean adipose cell volume, lipid, protein, and collagen content were measured in adipose tissue for 13 superficial and internal depots of 30 (25 males, 5 females) adult wild wolverines from the Northwest Territories of Canada (Pond et al., 1994). Analysis revealed no significant sex differences. Most adipose depots found in other terrestrial mammals were present in wolverines, and site-specific differences in adipose cell volume were comparable to other species. The largest adipose cells were found in the posterior (tissue caudal to the last rib) superficial and perirenal depots and the smallest in the intermuscular and cardiac depots. The posterior superficial depots contained a higher proportion of collagen than the anterior (tissue cranial to the last rib) superficial, intra-abdominal, and cardiac depots. The highest proportions of lipid were found in the posterior superficial and perirenal depots and the lowest in small inter-muscular and cardiac depots. No significant relationship was found between the concentration of lipid and non-collagen protein content of the adipose tissue between October and March. With the exception of cardiac adipose tissue, all other depots enlarged with increasing fatness (fatness = mass of all dissectible adipose tissue, except cardiac, expressed as a % of the estimated total body mass) and superficial depots expanded faster than internal depots. The partitioning of adiose tissue between total intra-abdominal and total superficial and between anterior and posterior superficial depots changed with fatness and were consistent with predictions from allometric equations derived from other carnivores. On the other hand, more than 70% of wolverines had 2–5 times as many adipose cells as predicted. Wolverines from the Northwest Territories thus appear to have both the physiological and anatomical ability to become obese; however, the energy reserves of many animals were found to be extremely low (Pond et al., 1994).

All four limbs of the wolverine are big and stocky, and the forelimbs are exceedingly powerful and used for digging, tearing, and turning rocks, logs, and carcasses. The feet are large and plantigrade. Digits four and three are the longest on the forefeet and hindfeet, respectively. Each paw has five toes with bear-like, strong, curved, semiretractile claws (Forsyth, 1985; Hash, 1987; Jackson, 1961; Wilson, 1982). The length of claws on the forepaws and hindpaws is 24–26 mm and 22–24 mm, respectively (Stroganov, 1969). The heavily furred, snowshoe-like paws bear a weight load of only 27–35 g/sq cm, giving the wolverine a locomotory advantage in soft and deep snow, and consequently enabling it to occasionally kill large ungulates such as moose (Haglund, 1974; Macdonald, 1985).

The gait of the wolverine is a sort of loping gallop. Tracks are wider than those of dogs and show the 5th toe, the hairiness of the sole, and the characteristic division of the sole pads of the front feet (Jackson, 1961). Forefeet of adults create circular tracks that may be 7–8 by 8–9 cm long (Hash, 1987). The hindfeet leave a distinctly longer track in the snow and lack the characteristic division of the primary sole pads of the forefeet (Jackson, 1961).

Wolverines, like many fissipeds and solitary animals with large home ranges, rely largely on olfactory communication (Koehler et al., 1980). Urine or scats are frequently deposited on trees, rocks, logs, and other prominent objects (Hash, 1987). Wolverines even deposit scent on coyote (*Canis latrans*) scent stations and near baited live-traps (Koehler et al., 1980). Scent glands are typically located on the face, tail, and especially around the anal region (Gorman and Trowbridge, 1989). In the Mustelidae, anal sacs are vesicular cutaneous invaginations opening by a short canal on either side of the anus or just internal to it. Anal musk glands of wolverines produce tannish yellow, highly odoriferous secretions characteristic of mustelids (Hash, 1987). Wolverines also possess ventral abdominal glands similar to those of martens; however, ventral glands of the wolverine have yet to be studied in detail (Hall, 1926; Hash, 1987).

In addition to the anal and abdominal glands, Buskirk et al. (1986) observed the presence of plantar glands on the surface of hind feet of the wolverine. They hypothesized that chemical transmission from these plantar glands may occur passively by means of ordinary locomotion; i.e., the chemical signal is left on surfaces contacted by the wolverines' hind feet. For a wide-ranging species like *Gulo*, plantar gland secretions represent a chemical signal that has a relatively low energy cost compared with most chemical signals; the adaptive value of this energy savings is apparent. A more complete histological study of these glands is needed (Buskirk et al., 1986).

Olfactory communication has certain advantages over other modalities: 1) scent marks can be used when visual or auditory signals are hard to detect; 2) chemical signals provide a spatial and historical record of an individual's movement; and 3) scent marks remain active for extended periods of time, even when the producer is not in the vicinity (Gorman and Trowbridge, 1989). Odorous chemicals may be synthesized by the animal itself, derived from the animal's diet, or produced from bacterial metabolism. Little information is available on the chemistry of social odors in carnivores (Gorman and Trowbridge, 1989).

Bacula of adult males are 80–90 mm in length and are straight except for the distal third which is curved approximately 15 or 20°. The bone is round or oval in cross section, and the tip expands into three prongs (Stroganov, 1969; Wright and Rausch, 1955). Bacula from adult ($n = 7$) and immature ($n = 13$) wolverines from northern Alaska weighed 1.8–2.9 g ($\bar{X} = 2.3$ g) and 0.7–1.5 g ($\bar{X} = 1.1$ g), respectively. The bone is less massive and the basal end less developed in immature males (Wright and Rausch, 1955). Testes of adult animals ($n = 25$) from the Yukon Territory varied in weight from 4 g in late fall and winter to about 17 g in spring (Rausch and Pearson, 1972).

Female wolverines have eight mammae (four abdominal and four inguinal; Jackson, 1961). Newborn young are altricial (Shilo and Tamarovskaya, 1981) but attain adult weight by about 7 months of age (Magoun, 1985), which demonstrates the large energy and nutrient contributions made by the mother (Banci and Harestad, 1988).

ONTOGENY AND REPRODUCTION. Wolverines are solitary animals; males and females are seen together only during the breeding season (Quick, 1953a). The mating system of wolverines appears to be polygamous (Rausch and Pearson, 1972). Females are believed to be monestrous and, in the wild, breed from May to August (Danilov, 1965; Magoun and Valkenburg, 1983; Pulliainen, 1968; Rausch and Pearson, 1972; Wright and Rausch, 1955). Recent studies of captive animals show that females generally come into estrus from June to early August; however, a pair of wolverines at the Dakota Zoo, North Dakota, U.S.A., bred on May 31 (Mehrer, 1976). Increased vaginal cornification occurs from mid-June through early July; this likely corresponds to the time when most matings occur in the wild (Mead et al., 1991).

Late-stage spermatids and spermatozoa are found in the testes as early as March (Mead et al., 1991). In adult captive wolverines ($n = 7$), maximal size of testes (2.6 cm by 2.0 cm) and elevated testosterone levels (3–5 ng/ml) were attained in early April and maintained through early July. Testicular regression began by late July and was complete by mid-August (Mead et al., 1991).

During the breeding season, males usually remain close to females, but females take the lead and initiate moves when pairs travel (Magoun, 1985). Typically, males will mount females from behind, with forelegs clasping the female's sides. The scruff of the female's neck is often grasped, particularly if she attempts to move (Magoun and Valkenburg, 1983). Magoun and Valkenburg (1983) did not observe any thrusting, although they suggest that it might occur shortly after the onset of copulation. Copulation appears to be highly variable: in Alaska, three wolverine pairs were observed copulating 4 times, for a minimum duration of 12, 20, 56 and 20 minutes, respectively (Magoun and Valkenburg, 1983). Ovulation is believed to be induced by coitus (Mead et al., 1993). Following copulation, both animals roll vigorously. The pair bond is usually broken after a few days (Magoun and Valkenburg, 1983).

Wolverines exhibit delayed implantation. Fertilized eggs remain in the blastocyst stage until nidation occurs, usually from November to March (Banci and Harestad, 1988). Only two published records of gestation time are available for captive wolverines. One female from the Copenhagen Zoo, Denmark, gave birth after a gestation period of 215 days, while another female from the Dakota Zoo, North Dakota, gave birth 272 days after copulation was observed (Mehrer, 1976). Post-implantation following nidation of the blastocyst is about 30–50 days (Mead et al., 1993; Rausch and Pearson, 1972).

Parturition occurs from January through April, with most females giving birth before late March (Myrberget and Sorumgård, 1979; Pulliainen, 1968). In northwestern Alaska, litter size ($n = 5$) averaged 1.75 young (Magoun, 1985). In Finland, mean litter size was 2.5 young ($n = 161$ litters), ranging from 1 to 4 (Pulliainen, 1968). In Norway and Sweden, litter size averaged 2.4 young ($n = 73$ litters; Haglund, 1966; Myrberget and Sorumgård, 1979). In Alaska and Yukon Territory, 54 females showed a higher productivity with a mean of 3.5 embryos per pregnancy (rangae 1–6; Rausch and Pearson, 1972). Five reproductive tracts collected in British Columbia revealed a mean of 2.6 embryos (Liskop et al., 1981), and six specimens from Montana had a mean of 2.2 embryos, the lowest reported for wolverines (Hornocker and Hash, 1981). Sex ratio of adults does not appear to differ significantly from 1:1; of 26 wolverines captured in northwestern Alaska, 12 males and 14 were females (Magoun, 1985). Similarly, seconary sex ratios do not appear to differ significantly from unity, for example 15 males: 22 females (Finland; Pulliainen, 1968), 35 males:48 females (Norway; Myrberget and Sorumgård, 1979), and 6 males:8 females (Alaska; Rausch and Pearson, 1972) have been reported.

Young are born fully furred with eyes closed and teeth not erupted. At birth their fur is white, they weigh an average of 84.0 g, and have a crown-rump length of 121.0 mm ($n = 3$; Davis, 1967). Young are weaned after 7–8 weeks (Myhre and Myrberget, 1975) and begin to accompany mothers on foraging trips in April or May (McCracken, 1985; Pulliainen, 1968). Adult size is often reached by early winter, and young disperse in November (McCracken, 1985; Rausch and Pearson, 1972). Some female wolverines attain sexual maturity at about 15 months of age and may produce their first litter when 2 years old. Similarly, most males were sexually mature at approximately 14–15 months of age, but some did not produce sperm until 26–27 months of age (Rausch and Pearson, 1972).

Wolverine young are raised exclusively by the female (Krott, 1960). Pulliainen (1968) reported instances of males visiting dens occupied by females in winter, but it seems dubious that males provide parental care (McCracken, 1985). In northwestern Alaska, males were oberved visiting females that were raising young from May through July (Magoun, 1985). Most likely, male visits to female dens may be related to curiosity or approach of the breeding season (Magoun, 1985; Rausch and Pearson, 1972).

ECOLOGY. Wolverines are opportunistic feeders and respond quickly to temporarily abundant or easily procurable food (Magoun, 1987). Van Zyll de Jong (1975) suggested that wolverines were morphologically and behaviorally adapted to a scavenging lifestyle, and indeed, carrion is an important food source of rwolverines throughout their range (Haglund, 1966; Hornocker and Hash, 1981; Krott, 1960; Magoun, 1987; Myhre and Myrberget, 1975; Pulliainen, 1968; Rausch and Pearson, 1972). Wolverines have been observed following both wolf (*Canis lupus*) and lynx (*Lynx lynx*) trails presumably to obtain the remains from kills made by these predators (Haglund, 1966; Myrberget, 1968).

Stomachs of 20 Alaskan wolverines showed moose and caribou (*Rangifer tarandus*) to be the most frequently consumed foods (Rausch, 1959). A vole (*Microtus* sp.) and ground squirrel (*Citellus undulatus*) were identified in a summer-killed wolverine, and snowshoe hare (*Lepus americanus*), northern red-backed voles (*Clethrionomys rutilus*), magpies (*Pica pica*), an unidentified hawk, and remains of a bird and fish were found in stomachs of winter-killed animals (Rausch, 1959). Porcupine (*Erethizon dorsatum*) quills have also been found both in stomachs and embedded in the flesh of several wolverine carcasses (Boles, 1977; Quick, 1953b; Rausch, 1959). Wolverines ($n = 193$) trapped or snared in Alaska revealed the following food items: moose, caribou, snowshoe hare, birds, microtines, beaver (*Castor canadensis*), lynx, and blueberries (*Vaccinium* sp.; Rausch and Pearson, 1972). The stomach of one wolverine from the Northwest Territories contained ptarmigan (*Lagopus* sp.; Boles, 1977). Along coastal Alaska, wolverines feed extensively on carcasses of whales, walrus (*Odobenus rosmarus*), and seals that have been washed ashore (Rausch and Pearson, 1972). In arctic Alaska, arctic ground squirrels (*Spermophilus parryi*) were the staple food in summer, while caribou carrion and cached squirrels were the primary diet in winter (Magoun, 1987). Elk (*Cervus elaphus*) and deer (*Odocoileus* sp.) constituted 15 and 27%, respectively, of the winter diet of wolverines from Montana. Domestic cow was present in 15% and horse in 10% of 56 scats collected; however, their presence was attributed to the baits of commercial trappers. Predation on hoary marmots (*Marmota caligata*) and snowshoe hare was also documented (Hornocker and Hash, 1981). Wolverines may prey heavily on Columbian ground squirrels (*Spermophilus columbianus*) when this prey is abundant (Hornocker and Hash, 1981). A case of cannibalism under unusual circumstances was reported in Jasper National Park, Canada, when four wolverines were accidently trapped in a drained wooden water tank (Flook and Rimmer, 1965).

In Norway, reindeer was the most important winter food, being present in 81.6% of the stomachs ($n = 76$; Myhre and Myrberget, 1975). Percent occurrence for other food types were: moose, 7.9%; roe deer (*Capreolus capreolus*), 2.6%; hare (*Lepus timidus*), 3.9%; small rodents, 14.5%; and birds, 6.6%. Wasp larvae also constituted a choice item when available (Krott, 1960). In Finland, remains of reindeer were present at seven dens, moose, red fox (*Vulpes vulpes*) and hares at two dens, and ptarmigan collected from hunter traps at one den (Pulliainen, 1968). In Sweden, lemmings were common food and shrews (*Sorex* sp.) were killed and occasionally eaten (Haglund, 1966).

A few early reports of wolverine attacks on big game animals are seemingly exaggerated (Grinnell, 1926; Soper, 1970). In some areas, confusion between the cougar and wolverine had led to erroneous reports. Guay (1986) presents an illustration of a cougar (*Felis concolor*) attacking a bull elk and mistakenly refers to it as a wolverine attacking a caribou (Prescott, 1987). Although wolverines have been known to successfully attack and kill big game such as caribou (Bjärvall, 1982; Burkholder, 1962; Haglund, 1974) and moose (Haglund, 1974), such predation is believed to occur only under specific snow conditions. While deep and powdery snow hinders the movements of ungulates, the large paws of wolverines enable them to travel easily under the same conditions. In Finland, wolverines were responsible for 25.4% of predation on captive reindeer between 1976 and 1983. Under conditions of crusted snow, wolverines were reported to kill both adult reindeer and their calves from February to April (Haglund, 1966; Nieminen and Leppäluoto, 1985). Similarly, in Siberia and Norway wolverines have killed reindeer, elk, and maral (*Moschus moschiferus*) in the latter part of winter (Haglund, 1966; Zyryanov, 1989). Under light snow conditions, wolverines tend to ignore big-game animals (Haglund, 1966). Wolverine predation on big game has not been documented in North America (Hornocker and Hash, 1981).

Wolverines most frequently kill larger prey by biting the back of the neck, the back itself, and the withers. In some instances, neck tendons are severed, and less frequently, prey are grabbed at the throat and choked (Haglund, 1966). Prey rarely escape after being seriously injured (Haglund, 1966).

Odor of wolverine urine suppresses feeding of black-tailed deer (*Odocoileus hemionus columbianus*) and snowshoe hare (Sullivan et al., 1985*a*,*b*). It is possible that a predator-prey relationship exists whereby prey species choose to avoid an area that is freshly marked by wolverines (Sullivan, 1986).

Habitat loss and predation by humans are the most important factors affecting wolverine numbers (Hornocker and Hash, 1981; Macdonald, 1985). A study in Montana revealed that 15 of 18 wolverine deaths were caused by humans. Furthermore, all adult wolverines captured had one or more toes missing and numerous broken teeth, presumably resulting from previous escapes (Hornocker and Hash, 1981; Shufeldt, 1924).

Wolves, black bears (*Ursus americanus*), brown bears, cougars, and golden eagles (*Aquila chrysaetos*) are capable of killing wolverines, particularly young and inexperienced individuals (Hornocker and Hash, 1981). One case of attempted predation on a wolverine in Montana was attributed to a cougar (Hornocker and Hash, 1981). Wolves, however, appear to be the wolverine's most important natural predator. Successful predation by wolves most commonly occurs when a cornered wolverine is unable to escape by climbing a tree, either because of absence of trees or because the animal is caught in a trap (Boles, 1977; Burkholder, 1962). Murie (1963) observed three cases of unsuccessful attacks on wolverines by wolves; in each case the wolverine escaped by climbing a tree. Interspecific food competition between these two predators may discourage their simultaneous use of the same area. Pulliainen (1965) believed that the arrival of a wolf in a wolverine's territory usually leads to the desertion of the area by the latter.

Non-human-related deaths in wild wolverines resulted from eating porcupine quills (Grinnell et al., 1937), "suppurative metritis" (an infection of the uterus probably related to a retained fetus), and starvation (Hornocker and Hash, 1981). Two cases of leg malformations were reported in one litter of wolverines (Pulliainen and Alfthan, 1967). In captive animals, teeth, throat infections, and tuberculosis are reported as causes of mortality (Woods, 1944).

Wolverines harbor numerous endoparasites including flukes (*Opisthorchis felineus*), tapeworms (*Bothriocephalus* sp. and *Taenia twitchelli*), and roundworms (*Dioctophyme renale* and *Soboliphyme baturini*; Erickson, 1946). In Alaska, 86% of examined wolverine carcasses ($n = 80$) were infested with one or several of the following trematode (*Alaria* sp.), cestodes (*Mesocestoides kirbyi* and *T. twitchelli*) and nematodes (*Trichinella spiralis, Molineus patens, Ascaris devosi*, and *Physaloptera torquata*). *T. twitchelli* inhabits the duodenum of infected wolverines and may use the porcupine as an intermediate host (Rausch, 1959). Additional parasites include nematodes (*Physaloptera sibrica*) found in Eurasian wolverines (Spasskii et al., 1952) and heartworm (*Dirofilaria immitis*) found in captive specimens in Michigan, U.S.A. (Williams and Dade, 1976). Ectoparasites include dog ticks (*Dermacentor variabilis*; Haugen, 1961), fleas (*Oropsylla alaskensis*; Haas et al., 1982), and the ear canker mite (*Otodectes cynotis*; Wilson and Zarnke, 1985).

The scavenging lifestyle of the wolverine dictates a solitary existence, large home range, and extensive seasonal movements (Hornocker et al., 1983). Adult wolverines do not defend territories, and home ranges may overlap between individuals of the same and opposite sex (Banci and Harestad, 1990; Hornocker and Hash, 1981; Whitman et al., 1986). In northwestern Alaska, most resident females maintained home ranges that excluded females other than offspring (Magoun, 1985). Males tolerate females but tend to be aggressive toward other males present in their home range (Krott, 1960). Resident adult male home ranges may overlap ranges of young males that have not yet dispersed (Magoun, 1985).

Throughout the distribution of the species, males have larger home ranges than females. The average yearly range of males and females, respectively, in northwestern Alaska was 666 km^2 (range: 488–917) and 103 km^2 (range: 53–232). During March through August, the average home range size of lactating females was 70 km^2 (range: 55–99) and of females without young was 97 km^2 (range: 68–178; Magoun, 1985). The average yearly ranges of males and females, respectively, in southcentral Alaska was 535 and 105 km^2 (Whitman et al., 1986), and in Montana 422 and 388 km^2 (Hornocker et al., 1983). In Montana, the largest home range recorded (963 km^2) was that of an adult female (Hornocker and Hash, 1981). Home-range size in the Yukon varied between 76 and 269 km^2 for females and between 209 and 269 km^2 for males (Banci and Harestad, 1990).

Male wolverines are more mobile than females, although both sexes travel long distances. Daily movements of > 30 km have been recorded in Europe (Haglund, 1966; Krott, 1960; Pulliainen, 1968). In Montana, straight-line distances between two consecutive relocations (10 days apart) was 10 km, while straight-line distance travelled in 3 days was 64 km for males and 38 km for females (Hornocker and Hash, 1981). A movement of approximately 300 km was recorded in Alaska and was attributed to dispersal (Magoun, 1985). Similarly, a 2-year-old male collared in Alaska was captured at a straight-line distance of 378 km from its capture location (Gardner et al., 1986). Food availability is generally considered the most important determinant of home-range size and movements of wolverines (Krott, 1960; Hornocker and Hash, 1981).

Wolverines are generally found in remote areas of undisturbed wilderness. In Montana, 70% of the relocations of radio-collared wolverines were in large areas of mature timber. The most commonly selected cover type was alpine fur forest (*Abies lasiocarpa*), but stands of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) were also frequently used. Wolverines were rarely found in burned areas or wet meadows. No individuals were located in clear-cuttings; however, tracks were observed crossing clear-cutting areas (Hornocker and Hash, 1981). In northerly environments, forests seem to be avoided in summer, while tundra is avoided in winter. Other habitats such as shrub, rock or ice, are used in proportion to their availability (Whitman et al., 1986). Telemetry data suggest that wolverines of both sexes move to higher elevations during the summer and to lower elevations in winter. These movements probably reflect variations in prey abundance (Hornocker and Hash, 1981; Whitman et al., 1986).

Densities of wolverines are never high (Makridin, 1964). Van Zyll de Jong (1975) noted that wolverines tend to be less abundant than wolves even in optimal habitats. Densities recorded for different locations vary from one wolverine/200 km^2 to one/500 km^2 in Scandinavia (Krott, 1959). Higher densities varying from one wolverine/50 km^2 to one wolverine/250 km^2 have been recorded in Siberia (Zyryanov, 1989). In North America, density was estimated to be one/200 km^2 in Alaska (Quick, 1953*a*), one/177 km^2 in the Yukon (Banci and Harestad, 1990), and one/65 km^2 in Montana (Hornocker and Hash, 1981).

Free-ranging wolverines have an average life expectancy of 4–6 years (Hash, 1987). Of 923 wolverines captured in Alaska and Yukon, the oldest animal was a 13-year-old female, and 15 animals were ≥ 10 years old (Rausch and Pearson, 1972). Average life span of 45 captive wolverines surviving longer than 6 months was 5.5 years (Woods, 1944). The oldest captive wolverine surpassed 17 years of age (Williams and Dade, 1976).

Wolverines are difficult to study because they inhabit remote wilderness areas, their movements are wide-ranging, and they occur at low densities. Telemetry studies generally require aircraft because most wolverines inhabit areas inaccessible by vehicle (Hornocker and Hash, 1981; Magoun and Valkenburg, 1983). When being handled, individuals are most commonly anesthetized with intramuscualr injection of ketamine hydrochloride (Hash and Hornocker, 1980), ethorphine HCl, or with a mixture of ethorphine HCl and xylazine HCl (Ballard et al., 1982).

Wolverines' space-use patterns link its conservation to the preservation of large tracts of undisturbed habitat (Pulliainen, 1988). In addition, strict harvest regulations in areas where wolverine populations remain should help ensure the long-term survival of this species (Wilson, 1982).

In the 16th and 17th century, wolverine pelts were highly prized and the Siberian city of Turinsk reputedly placed the wolverine in its coat of arms as a emblem of local commerce (Macdonald, 1985). Today, wolverine pelts are not economically important on the international market or in the fur industry, but are valued in Arctic and subarctic communities primarily for trim on parkas and other outer garments (Banfield, 1987; Hash, 1987; Jackson, 1961). The value of wolverine fur lies in the fact that it resists frosting more than wolf or coyote fur. Although ice crystals from a person's breath form on wolverine fur they can easily be brushed off and do not form chunks of ice (Allen, 1972; Peterson, 1966; Plitt Hardy, 1948; Quick, 1952). Prime pelts are valued as trophies for taxidermy purposes, prepared as wall mounts or rugs, and occasionally used for coats (Obbard, 1987).

BEHAVIOR. Adult wolverines are solitary except during the breeding season when males and females remain together for 2–3 days (Magoun, 1985). When not receptive, females react defensively if males try to get too close (Magoun and Valkenburg, 1983). Wolverines are playful animals (Krott, 1960). Play has been observed in solitary animals, with an object, between mated pairs, between siblings and dam, and between individuals that were probably familiar (Magoun, 1985). Play serves to exercise young animals' abilities to learn (Krott, 1960) and is important for pair bonding (Magoun and Valkenburg, 1983).

Diel activity of wolverines is variable; the animals are generally nocturnal, although some activity can occur during the day (Haglund, 1966; Pulliainen and Ovaskainen, 1975; Wilson, 1982). Krott (1960) reported activity periods of 3–4 h, interrupted by similar intervals of time devoted to sleep. Precipitation tends to reduce activity, while dry weather, full moon, bright auroras, or hunger usually increase activity. Wolverines are active throughout the year.

Construction of snow dens is generally similar among female wolverines. Entrance holes go straight down or spirally to ground level, and from there either end or follow along the ground for a short distance. Along the main corridor, short chambers are used as food stores or toilets (Myrberget, 1968). Dens are primarily used by females during parturition and lactation. Kits are often born in shallow (5–15 cm deep) pits dug in the ground. Dens may have one or more openings, and the length of the corridor varies from 1 to 40 m (Pulliainen, 1968). If disturbed, females may move their kits to a different location (Myrberget, 1968; Pulliainen, 1968).

Of 31 dens in Finland, 10 were in deep ravines on fells, 15 on gentle fell slopes (8 at timberline and 7 in alpine regions), and six were in spruce and pine peat-bogs (Pulliainen, 1968). In Finnish Lapland, dens were mainly dug in snow, in depth ranging from 1 to 3 m. Some dens were also dug under fallen or standing spruce trees, and in one case inside a hollow spruce (Pulliainen, 1968). In Norway, 15 out of 25 dens were in fell habitat in open mountain terrain, 8 were at tree border or in a higher birch (*Betula* sp.) forest, and 2 were in mixed birch and pine forest. All dens were between 200 and 1,500 m above sea level. Moreover, wolverine dens were mainly found on south or southwest exposures in the Scandinavian mountains (Myrberget, 1968). Resting beds can sometimes be holes dug under carcasses (Haglund, 1966).

Wolverines readily swim where lakes are abundant (Krott, 1960; Reed, 1956) and are also agile tree climbers (Grinnell, 1926; Krott, 1960; Murie, 1963). On occasion, an individual will rise on its hind feet to investigate a strange sound or a smell (Krott, 1960). Wolverines readily use trails made by snowmobiles and snowshoes in deep powdery snow (Haglund, 1966).

Foraging behavior of wolverines varies at different times of year. In spring and summer, wolverines tend to search for eggs of ground-nesting birds, larvae of wasps, and berries. If voles or lemmings are found, wolverines pounce on them in a mousing posture typical of other carnivores. Ground squirrels are chased until caught or until they escape. Wolverines dig for ground squirrels if the burrows are shallow, but rarely dig into extensive burrows. Food may be eaten immediately, eaten later, cached, or taken to kits (Magoun, 1985). Both male and female wolverines occasionally chase caribou in summer, but caribou appear to easily outdistance wolverines at this time of year. One cow with a calf attacked a wolverine, striking out at it with her front hooves (Magoun, 1985).

In winter, deep snow allows the wolverine to kill a variety of mammal species (Krott, 1960). In Sweden, wolverines have been observed repeatedly using their own trail from caches of meat to old kill sites (Haglund, 1966). Excellent senses of smell and hearing may be used for locating carcasses and live prey. The general hunting technique for big game animals is to chase opportunistically; hunting by stalking, followed by a surprise attack, is rare. Wolverines have been observed chasing reindeer for 1 km (Sweden; Haglund, 1966) and caribou for 8 km (Alaska; Magoun, 1985). Excess killing may occur if hunting conditions are unusually favorable; for example, a male wolverine that visited a reindeer feeding site on two occasions killed 7 individuals the first time and 10 the next (Haglund, 1966).

Excess food may be cached for later use. Food is generally cached in holes dug in the ground, but can also be hidden in trees (Haglund, 1966; Krott, 1960). Wells are also used for food storage by wolverines in Sweden. In northwestern Alaska, some food was cached under snowdrifts, but most was buried under a few centimeters of soil (Magoun, 1985). Wolverines were observed caching freshly killed ground squirrels by digging a hole in the ground, placing the carcass inside, then covering it with soil and vegetation. A caribou leg was cached by a male who used his nose to cover it with soil and vegetation. Most caches utilized in winter were probably made before the ground was frozen (Magoun, 1985). Wolverines also excavated caches made by red foxes and brown bears (Magoun, 1985). Food caching is believed to be especially important in the vicinity of parturition dens where food can be carried to the young. Females will also carry meat in their stomach for later regurgitation for the young (Haglund, 1966).

Scent marking is an important form of communication among wolverines (Koehler et al., 1980) and feces, urine, and glandular secretions are all used in object marking (Gorman and Trowbridge, 1989; Magoun, 1985). Wolverines have anal and abdominal glands similar to other members of the genus *Martes* (Ewer, 1973; Hall, 1926). Olfactory marking is achieved by rubbing the abdominal gland against available structures or depositing musk from the anal sacs. Wolverines frequently mark their home ranges; the large home ranges are difficult to defend against intruders, and thus, marking may serve to maintain the essentially solitary nature of the wolverine by providing a temporal and spatial record of an individual's movements (Gorman and Trowbridg, 1989; Koehler et al., 1980). In Montana, wolverines were found to mark at a rate of eight sites/km of travel. Preferred tree species for marking was the lodgepole pine (Koehler et al., 1980). Four marking methods were identified: (1) climbing a tree and depositing musk on the tree trunk or on the ground from the tree, (2) scratching the ground without depositing musk, (3) gnawing or biting a limb or root scented with musk, and (4) depositing a scat or musk on the ground without leaving other visual signs. The deposition of musk on the ground or on a tree trunk was by far the most common method of marking, being recorded on 70% of the 157 marked sites (Koehler et al., 1980). Wolverines rarely scent-marked while hunting, digging for prey, or eating (Magoun, 1985). Accounts of acoustic communication in this species are unavailable (Peters and Wozencraft, 1989).

GENETICS. *Gulo gulo* has a diploid number of 42 chromosomes; of these, 24 are meta- or submetacentric in shape, and 16 are acrocentric. The sex chromosomes are comprised of a metacentric X chromosome and an acrocentric Y (Hsu and Benirschke, 1970). In comparison, the fisher (*Martes pennanti*) and American marten (*M. americana*), have a diploid number of 38 chromosomes (Hsu and Benirschke, 1970; Wurster and Benirschke, 1968).

REMARKS. Throughout history, the wolverine has been regarded as a myserious creature. Legends often refer to the strength, ferocity, and cunning of the wolverine and it has probably inspired more fear, hatred, and awe than all other mustelids (Patent, 1973).

Gulo means huge eater or glutton (Kvam et al., 1988) and originated from the Latin word *gulosus* (Hash, 1987). The German name "vielfrass" is also believed to reflect the voracious appetite of the wolverine (Kvam et al., 1988). The wolverine is known by numerous vernacular names including glutton, carcajou, Indian devil, nag-gwy-gway (Chippewa), skunk bear, devil bear, and devil beast (Anthony, 1928; Danilov, 1965; Hash, 1987; Jackson, 1961; McCracken, 1985; Soper, 1964). The strong jaws and teeth of the wolverine and its substantial consumption of carrion have gained it the name "hyaena of the north" (Ewer, 1973).

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