Chapter 5

Wolverine

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INTRODUCTION

The wolverine (*Gulo gulo*) is the largest-bodied terrestrial mustelid. Its distribution is circumpolar; it occupies the tundra, taiga, and forest zones of North America and Eurasia (Wilson 1982). North American wolverines are considered the same species as those in Eurasia. They are usually thought of as creatures of northern wilderness and remote mountain ranges. In fact, wolverines extend as far south as California and Colorado and as far east as the coast of Labrador, although low densities are characteristic of the species.

Relative to smaller mustelids, the wolverine has a robust appearance, rather like a small bear. Its head is broad and rounded, with small eyes and short, rounded ears. The legs are short, with five toes on each foot. The claws are curved and semi-retractile and are used for climbing and digging. The skull and teeth are robust and the musculature, especially of the head, neck and shoulders, is well developed. These adaptations allow the wolverine to feed on frozen flesh and bone (Haglund 1966). Typical weights for adult males are 12-18 kg and for adult females, 8-12 kg. Adult males are 8-10% larger in measurements and 30-40% larger in weight than females.

The coat is typically a rich, glossy, dark brown. Two pale buff stripes sweep from the nape of the neck along the flanks to the base of the long, bushy tail. The fur on the abdomen is dark brown. White or orange patches are common on the chest or throat. Occasionally the toes, forepaws or legs are marked with white. Color can vary strikingly, even within the same geographical area, from a pale brown or buff with well defined lateral stripes to a dark brown or black with faint or no lateral stripes. Very blond or "white" wolverine are rare. Because of the extensive within-site color variation, geographical differences in color do not seem to be apparent, except for possibly greater incidence of white markings in some areas. Color does not vary markedly with season. A single visible moult extends from spring or early summer to autumn (Obbard 1987). Age and sex differences are seldom described, but Holbrow (1976) suggested that younger animals may be darker.

The wolverine has been characterized as one of North America's rarest mammals and least known large carnivores (table 1). Only four North American field studies have been completed: two in Alaska (Gardner 1985; Magoun 1985) and one each in the Yukon (Banci 1987) and Montana (Hornocker and Hash 1981). Additional studies, including one in Idaho, Alaska, and the Yukon are in progress (table 1). Reproduction and food habits of northern wolverine have been described from analyses of carcasses (table 1). Information on the habitat and population ecology of wolverines in the forests of western North America is mainly anecdotal or not available. Because of reductions in numbers and in distributions, increasing emphasis is being given in some western North American areas such as California, Colorado, and Vancouver Island, British Columbia, as to whether wolverine still occur. The paucity of information is largely due to the difficulty and expense of studying a solitary, secretive animal that is rare compared to other carnivores, and is usually found in remote places.

The wolverine's importance to humans began with the fur trade. Wolverine fur is renowned for its frost-resistant qualities (Quick 1952) and is sought for use as trim on parkas, especially by the Inuit of Canada and Alaska. Although wolverine fur typically is not used for making coats, it is commonly used in rugs and taxidermic mounts. The names by which wolverine are known are colorful and descriptive. The Cree names *ommeethatsees,* "one who likes to steal" and *ogaymotatowagu,* "one who steals fur" (Holbrow 1976), refer to wolverine raiding traplines, cabins and caches, and removing animals from traps. They are called "skunk-bears" because they mark the food they kill or claim, including the contents of cabins, with musk and urine. "Glutton" refers to its mytho-

Table 1.–The knowledge base for the wolverine in North America by subject. This includes studies for which the subject was a specific objective of the study; incidental observations are not included. Sample size Is number of animals studied, or for food habits, number of scats or gastrointestinal tract contents, unless stated otherwise. Sample sizes for dispersal include only juveniles. Theses and dissertations are not considered separately from reports and publications that report the same data. Individual studies are represented by (*) discounting redundancies.

Topic, author	Location	Method	Duration (years)	Sample size	Note
Home range & habitat use					
*Hornocker and Hash 1981	NW Montana	Telemetry	7	24	
*Gardner 1985	SC Alaska[1]	Telemetry	4	12	
*Magoun 1985	NW Alaska	Telemetry	4	19	
*Banci 1987	SW Yukon	Telemetry	4	10	
Demography					
*Wright & Rausch 1955	Alaska	Carcasses	4	33	
*Bausch & Pearson 1972	Alaska & Yukon	Carcasses	5	697	
*Llskop et al. 1981	N British Columbia	Carcasses	2	90	
Gardner 1985	SC Alaska[1]	Carcasses	3	71	
Magoun 1985	NW Alaska	Carcasses	4	67	
Band & Harestad 1988	Yukon	Carcasses	3	413	
Food Habits					
Rausch 1959	Alaska	Gut analysis	4 (winter)	20	Stomachs
Rausch & Pearson 1972	Alaska	Carcasses	5 (winter)	192	G.I. tracts
Hornocker & Hash 1981	NW Montana	Scats	6 (Dec-Apr)	56	# individuals unknown
Gardner 1985	SC Alaska[1]	Carcasses	4 (Dec-Mar)	35	Colons
Gardner 1985	SC Alaska[1]	Observations	3 (Apr-Oct)	9	Of 70 telemetry flights
Magoun 1985	NW Alaska	Scats	2 (Nov, Feb, Mar)	82	# individuals unknown
Magoun 1985	NW Alaska	Observations	4 (May-Aug)	48	Of 362 5-min. periods
Banci 1987	Yukon	Gut analysis	4 (Nov-Mar)	411	G. I. tracts
Dispersal					
Gardner 1985	SC Alaska[1]	Telemetry	4	2	2 males
Magoun 1985	NW Alaska	Telemetry	4	7	4 males
Banci 1987	SW Yukon	Telemetry	4	3	1 male
Natal Dens					
Magoun 1985	NW Alaska	Observations	4	4	3 females

[1] *Three field studies are currently In progress; Golden et al. 1993, south-central Alaska; Cooley, pers. comm., northern Yukon; Copeland 1993, north-central Idaho.*

logical voracious appetite and "Indian devil" to its importance in the legends of native cultures. The wolverine has been described as "the fiercest creature on earth" (Ferguson 1969), "vicious," a "dangerous killer," and "a fearless aggressive fighter" who "will drive bears away from their kills" (Winkley and Fallon 1974). This reputation as vicious and conflicts with trappers resulted in wolverine being considered as vermin by European-North Americans, an attitude that persisted into the 1960's.

The strength of the wolverine is legendary. Reports have it carrying away moose (*Alces alces*) carcasses and caribou (*Rangifer tarandus*) heads, destroying steel traps, and eating through wood walls and roofs. As a scavenger largely dependent on large mammal carrion, the wolverine needs the tenacity to survive long periods without food and the strength to use available food. Not a hunter, it depends on wolves and other predators to provide carrion, and contrary to legend, is at times killed by these carnivores.

Within its geographic range, the wolverine occupies a variety of habitats. However, a general trait of areas occupied by wolverines is their remoteness from humans and human developments. The wolverine is a management and conservation enigma because the attributes of wilderness upon which it depends are not known. Is food, denning habitat, solitude, or some other factor all-important? Some disturbed habitats have abundant food in the form of large mammal carrion but do not support wolverines. Wolverines can move long distances but have not recolonized Labrador and Quebec despite the abundance of caribou and undisturbed habitat. By contrast, wolverines in arctic Alaska can survive

some winters with their only food the remnants of old caribou kills, long after the caribou have migrated elsewhere.

Human presence alone is not a deterrent to the presence of wolverines, as evidenced by their feeding in garbage dumps in northern Canadian communities. If large tracts of undeveloped and unroaded habitat are essential, why do wolverine occur in the logged forests of the Sub-Boreal Interior of British Columbia and in the habitats criss-crossed with seismic lines on the Boreal Plains? (See map in Appendix A.) A combination of factors likely underlie the presence or absence of self-sustaining wolverine populations. A pressing conservation issue is that we lack knowledge of what factors allow wolverines to persist at intermediate densities in western Canadian forests, while resource managers are being asked to provide for the needs of wolverines in the western conterminous United States, where population and habitat conditions are poorly known and likely more tenuous.

CURRENT MANAGEMENT STATUS

In the United States, wolverines may be trapped for fur only in Alaska and in Montana, but in Canada, they are important furbearers in all western provinces and territories and in Ontario. Trapping seasons generally extend from October-November to February-April; seasons are longest in the North. The wolverine population east of Hudson Bay has been classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 1993). Harvests in Ontario are minimal and mostly incidental, in traps set for other species.

In most jurisdictions where they are trapped, wolverines have dual status as a furbearer and as big game, but hunting is an important source of mortality only in the northern Yukon, the Northwest Territories, and Alaska. Reported harvests from Alaska and the Canadian territories likely account for only one-fifth to one-third of the total harvest because of heavy unreported harvest and use by local communities (Melchoir et al. 1987). The requirement to submit pelts for sealing in the Yukon is recent and its effectiveness is unknown. Declining wolverine harvest trends throughout southcentral Alaska during the 1980's prompted managers to reduce season lengths and bag limits and to restrict harvest methods (unpublished data in Gardner et al. 1993; Becker and Gardner 1992). Concerns about overharvests have also been expressed in other areas of Alaska (unpublished data in Bangs and Bailey 1987).

Management of furbearers in British Columbia, the Yukon, and the northern parts of the prairie provinces is based on a system of registered traplines, on which individual trappers or bands are given the exclusive right to trap. This system reduces trapper effort, avoids localized over-harvests, and provides trappers with an incentive to harvest sustainably. Trapping is not permitted in national, provincial, or territorial parks. Harvests in British Columbia are monitored by mandatory reporting of furs sold by trapline. Harvesting of wolverine on Vancouver Island is prohibited. Beginning in 1993-94, seasons in southwestern British Columbia were closed, consistent with the view that furbearer populations at low densities in marginal habitats should not be trapped.

In Alberta, the southern and agricultural parts of the province are closed to wolverine trapping. Most (80-90%) of the yearly harvest in Alberta and Saskatchewan is incidental to harvests of other species, or wolverine are taken opportunistically by big game hunters (F. Neumann, W. Runge, pers. comm.). Similarly in Manitoba, 35-44% of the harvest is incidental (I. McKay, pers. comm.). In the Northwest Territories, voluntary carcass submission is used to monitor the age-sex composition of the harvest (unpublished data in Poole 1991-1992). In the Yukon (B. Slough, pers. comm.), Alberta (unpublished data in McFetridge 1991-1993), and British Columbia (unpublished data in Rollins 1993), annual trapper questionnaires are used to monitor trends in furbearer and prey abundance.

Conterminous United States

The wolverine is designated as threatened in California, endangered in Colorado, and protected in four states (Appendix C, table 4d). Petitions have been filed for listing under the U.S. Endangered Species Act for California and Idaho. It is listed by the USDA Forest Service, Regions 1, 2 ,4, and 6 as a sensitive species (Appendix C).

Other than Alaska, Montana is the only state that allows trapping of wolverines. Before 1975, the wolverine in Montana was classified as a predator and unprotected (Hornocker and Hash 1981). Since then, trapping has been limited by seasons, licensing, and a seasonal limit of one wolverine per trapper. These regulations decreased the annual harvest "markedly" (Hornocker and Hash 1981). Most of the current trap-

per harvest in Montana is believed to be incidental, in sets for other furbearers (B. Giddings, pers. comm.).

DISTRIBUTION AND TAXONOMY

Wolverines in North America are more or less a continuous breeding group from the 38th parallel northward. Because of the wolverine's extensive movements, I have used ecoprovinces (Appendix A) for examining biological variation among wolverine populations. This convention is a convenience for delineating populations on an ecological basis. It is not known whether genetic differences occur among such populations or whether they can be considered ecotypes.

Distribution

Wolverines occur across the boreal and tundra zones of Eurasia. Populations in Scandinavia have recovered from near extinction in the last two decades (Bevanger 1992; Kvam et al. 1984). However, their future is uncertain because of increasing conflicts with sheep ranchers (Bevanger 1992). Ognev (1935) believed that the distribution of wolverines in Soviet states had decreased since the 1800's, but we know little about their current status there and in other Asian countries.

In the western conterminous United States, wolverines occur in peninsular extensions of the more extensive Canadian habitat, found mostly in the Humid Continental Highlands, Semi-Arid Steppe Highlands, Temperate Semi-Desert Highlands, and Mediterranean Highlands ecodivisions (Appendix A). They appear to have been rare or absent from the Columbia Plateau, Great Basin, Wyoming Basins, and Northern Great Plains ecoprovinces, and rare within the Canadian Prairie ecoprovince in historical times (Scotter 1964).

Seton (1929) concluded that the wolverine never occurred in Nova Scotia or on Prince Edward Island and that it disappeared from New Brunswick in the second half of the 19th century. Historically, wolverines occupied Labrador and Quebec (Kelsall 1981) but not Newfoundland Island (Anderson 1946). Wolverines are thought to have had a wide presettlement distribution in the Great Lakes region, although only in small numbers (deVos 1964). They have been absent from this region since the early 1900's (deVos 1964) and are extirpated from North Dakota, Minnesota, Wisconsin, Michigan, and Iowa (Hamilton and Fox 1987). Considering the extensive movements of wolverines, it is likely that individuals have been observed in areas that could not support home ranges or reproduction.

Wolverines in the Manitoba part of the Aspen Parkland ecoprovince (Appendix A) were rare (van Zyll de Jong 1975), and those in the Alberta part had disappeared by the early 1930's (Soper 1964). The wolverine's current range in Manitoba, generally north of 54°, includes much of the estimated range in 1909 (Seton 1909) but excludes areas that have been farmed or cleared. The distribution in northern Saskatchewan coincides with that of barren-ground caribou-the southern Taiga Shield ecoprovince and the forests of the Boreal Plains (W. Runge, pers. comm.). Wolverines in Alberta have been extirpated from the extensively modified Boreal Plains and currently only occur in the Taiga Plains and Shining Mountains ecoprovinces. In the latter, populations coincide with and may have been maintained by the extensive system of national parks: Jasper, Banff, and Waterton Lakes. Wolverines occur throughout mainland British Columbia, except for the southern agricultural areas. Self-sustaining populations likely did not occur in the Thompson-Okanogan Highlands ecoprovince.

Wolverines occur throughout the Yukon Territory, with an estimated 4,200 south of 66° (Banci 1987) and throughout mainland Northwest Territories. They occur continuously in mainland Alaska (LeReseche and Hinman 1973) but on only some of the southeastern islands. Records from the Canadian arctic islands are spatially and temporally sporadic. Wolverines have been reported from Victoria, King William, Winter, Melville, Ellesmere, Little Cornwallis, and Baffin Islands (Manning 1943; Anderson 1946; Holbrow 1976). These sightings likely indicate occasional animals, rather than self-sustaining populations, that have wandered in search of resources.

The presettlement geographic range of wolverines extended southward from Canada through the montane ecoregions to Arizona and New Mexico (Hash 1987). However, it is not known whether these southern occurrences represent reproducing populations or dispersers. Wilson (1982) noted that wolverines at the southern edge of their distribution were limited to montane boreal regions, with conspicuous gaps in the Basin and Plains ecoprovinces. The Thompson-Okanogan Highlands and the Central Rocky Mountain Basins ecoprovinces also were gaps in the distribution, despite occasional records. The northward retreat of wolverine distribution in the United

States began in the 1840's (Hash 1987). Today wolverines occur in Montana, Idaho, Wyoming, Colorado, Washington, Oregon, and California (Appendix B).

Montana

Wolverine populations in Montana were near extinction by 1920 (Newby and Wright 1955). However, numbers increased in the western part of the state from 1950 to 1980 (Newby and McDougal 1964; Hornocker and Hash 1981). Newby and Wright (1955) and Newby and McDougal (1964) believed this increase was due to increasing numbers of wolverines dispersing from Canada and later from Glacier National Park. Reduced trapping seasons on American martens (*Martes americana*) also aided this expansion by reducing trapping activity, as did low fur prices for wolverines and for lynx (*Lynx canadensis*) (Hash 1987).

Idaho

Reports in the mid 1930's and 1940's suggested that wolverines mostly occurred in the inaccessible mountains in the center of the state (Davis 1939; Rust 1946). Records in the late 1940's came from the northern panhandle (Pengelley 1951). Nowak (1973) reported several animals taken from the central mountains, apparently reflecting a comeback. The present distribution includes mountainous areas from the South Fork of the Boise River north to the Canadian border (Groves 1988). Groves (1988) concluded that wolverine occurred mostly in the Selkirk Mountains and the Sawtooth Mountain-Smokey Mountain complex.

Wyoming

Skinner (1927) estimated the Yellowstone population at 6 or 8 and believed that it was near extinction. Newby and McDougal (1964) believed wolverine had expanded their range into the southwestern part of the state, as did Hoak et al. (1982). There are 100 records available from 1961 to 1991, all in the western third of the state (unpublished data in Maj and Garton 1992).

Colorado

Grinnell (1926) reported a few wolverines "as far south as southern Colorado in the high mountains" and wrote of three captures in the southeast and northeast parts of the state. These latter records likely were of dispersers. Armstrong (1972) listed many old records from western Colorado but could locate only one specimen. Nowak (1973) recorded a specimen from south of Denver in 1965 and mentioned other sight records. Nead et al. (1985) doubted that wolverines were historically common in Colorado and suggested that current numbers were not self-sustaining.

Washington

Scheffer (1938) concluded that the few wolverines in Washington were individuals wandering from Canada. Some records in atypical habitats indicate dispersing wolverines, such as a male that was trapped in the center of the Okanogan Valley (Scheffer 1941). After no records in the state for over 20 years, three wolverines, all adult males, were killed and another seen in central and southern counties in 1964 and 1965 (Patterson and Bowhay 1968). Johnson (1977) suggested that wolverines were present in the Cascade Range between 1890 and 1919 but absent or rare throughout the state from 1920 through 1959. He believed they expanded their range in the 1960's and 1970's by dispersal from Canada. There are 28 records for the state for the period 1970 to 1990 (unpublished data in Maj and Garton 1992); their current distribution is not known.

Oregon

Bailey (1936) reported wolverines to be rare in Oregon. Kebbe (1966) referred to unverified reports that indicated that a remnant population existed in remote areas of the Cascade Range. Patterson and Bowhay (1968) referred to an unpublished report of an adult male killed in the Cascades in 1965, the first authentic record since 1912. Yocum (1973) suggested that the species had increased in abundance since the late 1950's. There are 23 records from 1981 to 1992, compared to 57 records from 1913 to 1980 (unpublished data in Maj and Garton 1992); the current status in the state is not known.

California

The historic range of the wolverine in California included much of the Sierra Nevada ecoprovince (Grinnell et al. 1937; Schempf and White 1977). Wolverines were believed near extinction in the early 1920's (Dixon 1925; Fry 1923). Jones (1950) concluded that the species was still rare and declining. Yocum (1973, 1974) believed that wolverines were becoming established in the mountainous areas of northwestern California, from "surviving nuclei" to the north. The current range includes a broad arc from

Del Norte and Trinity counties through Siskiyou and Shasta counties, and south through the Sierra Nevada to Tulare County (Schempf and White 1977). Reports in Kovach (1981) expanded this range to include the White Mountains.

Dispersal Corridors

Wolverines in the southern part of the Pacific Northwest Coast and Mountains ecoprovince are becoming isolated from the northern portion of the ecoprovince by heavy development in British Columbia. However, occasional reports within the Thomson-Okanogan Highlands ecoprovince of British Columbia and Washington suggest that this may be a dispersal corridor. It is also possible that wolverines have become isolated within the Sierra Nevada ecoprovince of California because of human activities.

Wolverines in the Colorado Rocky Mountains ecoprovince are isolated from areas to the north by the Central Rocky Mountain and Wyoming Basins (unpublished data in Maj and Garton 1992). These basins are arid and have been altered by human land uses. Geographic isolation of wolverines may seem unlikely because of their extensive movements. However, whether animals moving long distances successfully complete dispersal and reproduce is not known. Ecotypic variation over the geographic ranges of other large carnivores has been shown with DNA analyses (Fain in press; Knudsen and Allendorf in press) but is poorly known for the wolverine.

Taxonomy and Morphological Variability

Most authorities consider all wolverines in North America and Eurasia to belong to a single species (*Gulo gulo*) (Ognev 1935; Anderson 1946; Rausch 1953; Kurten and Rausch 1959; Krott 1960; Corbet 1966). Subspecific designations have been recognized to varying degrees. Hall and Kelson (1959) recognized *G. gulo katschemakensis* from the Kenai Peninsula, Alaska, but Dagg and Campbell (unpublished data 1974) considered this subspecies invalid. The Pacific wolverine, *G. gulo luteus,* was first described by Elliot (1903) from California and Grinnell et al. (1937) recognized this as a southern subspecies on the basis of skull characteristics alone. Further evidence to support a subspecific classification for the Pacific wolverine has not emerged. In an evaluation of the status of *G. gulo vancouverensis,* skulls of the Vancouver island wolverine (Banci 1982) differed in size and shape from those on the British Columbian mainland, although the comparison was based on a small sample. However, these mainland wolverines also differed from those in the Yukon, two populations that likely interbreed. Further, ecotypic variation was reflected in at least three regional mainland populations (Banci 1982).

Variation in body size of wolverines suggests ecotypic variation. Adult females in the Southern Arctic ecoprovince are the largest (K. Poole, pers. comm.). The smallest adult females occur in the Northern Rocky Mountain Forest, the Pacific Northwest Coast and Mountains, and the Shining Mountains ecoprovinces. In general, the most sexually dimorphic wolverines occur in the south and the least in the north. These results are consistent with those of Banci (1982), who found that skull measurements that differentiated among geographic areas differed by sex.

Management Considerations

1. Wolverines were widespread but likely occurred at low densities in the western conterminous United States in presettlement times. Areas that supported reproduction then are not known.

2. Wolverines are difficult to observe, even where they are relatively abundant. Frequency of sightings may not reflect population size but can result from greater human access to wolverine range. Wolverines can travel long distances and sightings may not indicate reproducing populations. Conversely, a lack of sightings does not mean a lack of presence. The presence or absence of wolverines needs to be confirmed in the field with the use of remote cameras or confirmations of tracks if information on their presence is important to managers.

3. Wolverines occupying different ecoprovinces differ in body size and behavior. This variation may represent local adaptation and may have important conservation implications.

Research Needs

1. Determine genetic diversity among wolverine populations. This information will assist in recovery programs.

2. Determine whether wolverine populations in the conterminous United States are self-sustaining or dependent on emigration from Canada.

POPULATION ECOLOGY

Reproduction and Natality

Wolverines exhibit delayed implantation, during which development of the embryo is arrested at the blastocyst stage. Implantation in the uterine wall can occur as early as November (Banci and Harestad 1988) or as late as March (Rausch and Pearson 1972). Because active gestation lasts 30-40 days (Rausch and Pearson 1972), birth can therefore occur as early as January or as late as April (Banci and Harestad 1988). For many mammals, winter may be an inhospitable time to give birth. However, ungulate carrion may be more plentiful in winter, which may favor parturition at that time in wolverines. Parturition in Norway was shown to correspond closely with the period when reindeer were most vulnerable (Haglund 1966; Roskaft 1990). Security cover for kits may also be enhanced during winter; snow tunnels or snow caves are characteristic natal and maternal dens for wolverine in many areas.

Females do not breed their first summer (Rausch and Pearson 1972; Liskop et al. 1981; Magoun 1985; Banci and Harestad 1988) and authors have reported varying proportions of the subadult age class (1-2 years) that breed. Banci and Harestad (1988) reported 7% in the Yukon, contrasting with the 50% reported by Rausch and Pearson (1972) in Alaska and the Yukon, and 85% reported by Liskop et al. (1981) for British Columbia. Differences in how wolverine ages were classed make comparisons among studies difficult; the subadult age class in the latter two studies may have included adults. Most males are sexually immature until 2+ years of age (Rausch and Pearson 1972; Banci and Harestad 1988). Testis weights increase throughout the winter (Rausch and Pearson 1972; Liskop et al. 1981; Banci and Harestad 1988) and by March, all adult males are in breeding condition (Liskop et al. 1981). Rausch and Pearson (1972) reported a peak in testis weights in June, presumably indicating the peak in breeding activity.

Reproductive Rates

Increasing litter sizes with age are important factors in productivity (Banci and Harestad 1988), as is common for mammals (Caughley 1977). For the Yukon, mean numbers of corpora lutea per female ranged from 3.1 for 2- to 3-year-old animals to 4.4 for those older than 6 years (Banci and Harestad 1988). Numbers of corpora lutea overestimated numbers of fetuses, whereas numbers of placental scars did not differ from those of fetuses (Band and Harestad 1988). Litter sizes as large as six in captive animals (Rausch and Pearson 1972) and four in wild ones have been reported. Litter size after den abandonment is typically fewer than three (Pulliainen 1968; Magoun 1985).

The proportion of adult female carcasses that were pregnant was 74% in the Yukon (Band and Harestad 1988), less than the 92% found in Alaska and the Yukon (Rausch and Pearson 1972) and 88% in British Columbia (Liskop et al. 1981). In the Yukon, the proportion of females that were pregnant in age classes 2-3 to 5-6 years ranged from 92% to 53%, respectively, but was 37% for females older than 6 years. Older females may be capable of larger litters, but fewer females in these older age classes may produce litters. In northwest Alaska, during a year when food was scarce because caribou were uncommon, none of four collared adult females were known to have produced young (Magoun 1985). In the 13 collective years of sexual maturity during which 6 adult females were observed, young were produced in only 5 years of wolverine life (Magoun 1985). In Montana, an adult female produced no young in the 3 years she was observed and only 50% of adult females were thought to be pregnant in any year of the 5-year study (Hornocker and Hash 1981). Two of 3 adult females in southwest Yukon did not reproduce young over the 3 years of that study (Band 1987).

The incidence of nonpregnant females appears to be related to nutritional status and the demands of lactation. Kits are weaned at 9-10 weeks (Krott 1960; Iversen 1972). The basal metabolic rate of wolverines during these first months of life increases in proportion to body weight raised to the 1.41 power ($W^{1.41}$) (Iversen 1972), higher than reported for other mammals where total heat production prior to weaning increases in proportion to body weight ($W^{1.0}$). Iversen (1972) suggested that the rapid increase in total heat production during the early phase of growth resulted from a faster growth of the high energy-producing tissues compared to other mammals. Young wolverines grow quickly after weaning and by 7 months of age have achieved adult size (Magoun 1985). The rapid growth of kits before and after weaning presumably places high energetic demands on mothers and can affect female reproduction in the immediate future (Band 1987).

Adult females appear to breed, but not necessarily whelp, yearly (Magoun 1985). Loss of young likely

occurs early in active pregnancy (Banci and Harestad 1988). The condition of females before implantation may be the most critical factor determining successful birth, but not survival of young. Although sample sizes were small (n = 5), Magoun (1985) observed some neonatal (preweaning) mortality.

Sampling Problems and Population Characteristics

Estimates of age and sex composition of wild populations have suffered from small sample sizes. The sex ratio is generally 1:1 (table 2). Sex ratios biased toward males were observed in northern Yukon and southcentral Alaska, where it was suspected that the capturing method, darting from helicopters during March, excluded denning females (D. Cooley, pers. comm.; Magoun 1985). The exclusion of females in a sample will also bias age ratios toward adults because young females exhibit a fidelity to the natal area that young males do not (Magoun 1985). The proportion of captured wolverines that were adults in northern Yukon and southcentral Alaska studies, 76% and 86%, respectively, were the highest of all studies (table 2).

Only studies in Idaho (unpublished data in Copeland 1993), southwest Yukon (Banci 1987), northwest Alaska (Magoun 1985), and Montana (Hornocker and Hash 1981) likely reflect the true demography of residents. The results of these studies were similar. The sex ratio was close to 1:1 in all studies. The proportion of adults ranged from 68% to 73%. More subadults occurred in northwest Alaska; however, subadult and young-of-the-year age classes were based on small samples in all studies. The proportion of juvenile wolverines, especially males, is likely to be the most variable among studies of unexploited wolverine populations. The longer a study and the more effort placed into tagging and following juveniles, the greater the accuracy in estimating the proportion of the population in this age class prior to dispersal.

Collecting information on transients is inherently difficult. Males disperse as young of the year or as subadults (Gardner 1985; Banci 1987), or at 2 years of age (Gardner 1985). Female offspring tend to remain close to their mother's home range (Magoun 1985), although some also disperse. Thus, the transient segment of the wolverine population is most likely composed, in decreasing proportions, of juvenile males, juvenile females, and adult males. The proportion of wolverines that are transient in any year varies with kit production, survival of neonates, and mortality. This transient segment likely plays an important role in maintaining the distribution and population characteristics of wolverines.

Estimates of wolverine densities are difficult to compare among studies because of inconsistent methods. However, two techniques show promise: (1) where aerial surveys are feasible, estimation based on probability sampling (unpublished data in Becker and Gardner 1992) and (2) in forested areas, remote cameras at bait stations (unpublished data in Copeland 1993). Because unique markings often allow the individual identification of wolverines, the latter has promise for mark-recapture as well as for detection.

Natural Mortality

Wolverines have few natural predators but are occasionally attacked and killed, but seldom eaten, by

Table 2.-Sex and age composition of resident wolverine in telemetry studies in North America, excluding dependent kits.

Location	Sex Ratio M:F	(*n*)	% Young of year	% Subadult	% Adult[1]	*n*	Reference
SW Yukon	1.0:1	(5:5)	20% (3)	7% (1)	73% (11)	15	Banci 1987[2]
NW Alaska	0.8:1	(10:12)	17% (3)	17% (3)	68% (13)	19	Magoun 1985[3]
NW Montana	0.9:1	(11:13)		29% (7)	71% (17)	24	Hornocker and Hash 1981[4]
N Yukon	2.5:1	(10:4)	(1) 7%	7% (1)	86% (12)	14	D. Cooley, pers. comm.
SC Alaska	2.4:1	(12:5)		24% (4)	76% (13)	17	Whitman and Ballard 1983[5]
NC Idaho	1.2:1	(6:5)	0%	27% (3)	73% (8)	11	Copeland 1993, unpubl.

[1] Young-of-the-year 0-1 years, subadult 1-2 years, adult 2+ years.
[2] Including 5 unmarked residents.
[3] Sex ratio includes 2 wolverine of unknown age.
[4] Subodult age group not differentiated into yearling and subadult. Method of aging not indicated; likely visual inspection and not cementum analysis.
[5] Ages based on subjective estimate of tooth wear; one unknown male classed as adult because of large weight, 17.7 kg. This study is a continuation of Gardner 1985.

wolves and other large carnivores (table 3, Burkholder 1962; Boles 1977; unpublished data in Gill 1978; Banci 1987). Hornocker and Hash (1981) described injuries they believed had been inflicted by a cougar (*Felis concolor*) and suggested that bears and eagles could kill wolverines, especially kits. The importance of predation on wolverine kits has not been documented. Wolverine mothers go to great lengths to find secure dens for their young, suggesting that predation may be important. Although not documented, adult males may kill kits. Magoun (1985) observed males visiting females with young prior to breeding, and on one occasion a male occupied the natal den of a female and her kit. Assuming that the turnover of resident males were high, a male would increase his fitness by killing kits that he likely did not sire. He would not only be killing another male's progeny, but be increasing the possibility that the female would successfully raise his kits the next year. This is because the death of her kits would improve her physiological condition through the early cessation of lactation.

Some wolverines, especially males, may be killed by conspecifics. Males in northwest Alaska had fresh wounds on their heads when captured in April, suggesting that the approach of the breeding season increases aggressive behavior (Magoun 1985). Altercations between young males and adult males may be the proximate encouragement for the former to disperse (Banci 1987).

Starvation likely is an important mortality factor for young and very old wolverines. Suspected deaths from starvation include two young-of-the-year females in southwest Yukon (Banci 1987) and a young female and an old male in Montana (Hornocker and Hash 1981). These animals relied heavily on baits just before their deaths, suggesting that very young and old age classes may be unsuccessful foragers, even if food is abundant (Hornocker and Hash 1981; Banci 1987). Documenting the fates of young males is difficult because of their extensive movements and it is not possible to predict whether sexes differ in their susceptibility to starvation.

The age-specific mortality reported in studies of collared wolverines (table 3) was 57% for adults, 7% for subadults, and 36% for young of the year. However, the mortality rates of juvenile wolverines are underestimated in these studies. The long distances covered by young of the year and subadults, especially males, makes it difficult to ascertain their fates unless they are trapped and their deaths reported. Mortality in these young age classes likely is substantial. Transients likely have a higher mortality rate than residents because they do not benefit from hunting in familiar home ranges. So, they likely have a greater chance of starvation, of being killed by conspecifics and of encountering traps. Krott (1982) believed that one-third to one-half of subadult wolverines perished during dispersal.

Table 3.--Fates of radio-collared wolverine.

			Cause of mortality							
Location	n	Years studied	Harvest	Starvation	Predation	Other	Unknown	Total	Annual %	Reference
NW Alaska	24	5	3					3	2.5	Magoun 1985
SC Alaska	16	3	2				1	3	6.2[1]	Whitman & Ballard 1983
SW Yukon	10	3	2	2	1	1		6	20.0[2]	Banci 1985
NW Montana	24	5	5	2		1		8	6.7[3]	Hornocker & Hash 1981
NC Idaho	11	1			1		1	2	18.1[4]	Copeland 1993, unpubl.
Total	86		12	4	2	2	2	22	10.6[5]	
% of total mortality			54%	18%	9%	9%	9%			

[1] *Status of 12 of the 16 wolverine unknown, 1 capture mortality not included.*

[2] *"Predator" = wolf; "other" = parasitic pneumonia, a female believed to be nutritionally stressed after raising young.*

[3] *"Other" = old female, suppurative metritis, uterus was badly infected; an additional 10 mortalities of unmarked wolverine occurred during the study, all from trapping.*

[4] *Two kits not included, one of which died from a capture-related cause; "predator" unknown; other = "old" female wolverine that had become habituated to trap bait; status of 1 male unknown.*

[5] *Mean of 5 annual mortality rates; harvest mortality represents an annual mean of 5.3% and natural mortality, 5.3%.*

Trapping Mortality

Over most of its distribution, the primary mortality factor for the wolverines is trapping (trapping and hunting mortality are considered together in this section). In telemetry studies, trapping has accounted for over half of all mortalities, although only two of the five study populations were trapped and the Montana study area was only trapped for the first 2 years of the 5-year study (table 3, Hornocker and Hash 1981). Most of these deaths were of animals that left the nonharvested study areas.

The cumulative impacts of trapping, habitat alterations, forest harvesting, and forest access on wolverines are not understood. Trapping can have important implications for conservation. Ensuring that a recovering population is protected from trapping must be accompanied by monitoring of trapping impacts on potential dispersers from surrounding populations.

Harvest data can provide insights into the vulnerability of age and sex classes. However, without information on the proportion of the population being harvested, on natural mortality, and on the additive or compensatory nature of trapping mortality, little can be said about the sustainability of such harvests. Harvests of juvenile wolverines, especially early in the season, likely are compensatory because of their suspected high natural mortality. Some harvests of adults, those that are nutritionally stressed, also will be compensatory. But, in general, I believe that the harvest of most adults is additive to natural mortality.

In one of the few attempts to estimate the sustainability of wolverine harvests, Gardner et al. (unpublished data 1993) used demographic data from radio-telemetry studies in Alaska and the Yukon (Banci 1987; Gardner 1985; Magoun 1985) in conjunction with density estimates (unpublished data in Becker and Gardner 1992) and harvest sex-age compositions (Gardner 1985; Banci 1987) to construct a population model. The annual sustainable harvest was an estimated 7-8% of the fall population. Recent wolverine harvests in parts of Alaska have exceeded 10% (unpublished data in Gardner et al. 1993).

Density and Population Trends

In general, wolverine densities are low relative to carnivores of similar size, although there can be a tremendous range, from 40 km^2 to 800 km^2 per wolverine (table 4). Annual trapper questionnaires have been used in the Yukon, British Columbia, and Alberta to determine furbearer population trends and factors responsible for changes in population status (B. Slough, pers. comm.; unpublished data in Rollins 1993; unpublished data in McFetridge 1993-1991). These surveys have indicated that over the past 4 years, wolverine populations have decreased in the Boreal Uplands, Sub-Boreal Interior, Central British Columbia Plateaus, Thompson-Okanogan Highlands, and Shining Mountains ecoprovinces, despite a general decrease in trapper effort. These ecoprovinces are characterized by extensive forest harvesting, as well as oil and gas exploration in the Boreal Uplands, ranching in the Central British Columbia Plateaus, and increasing human settlement and roadbuilding, especially in southern Canada.

Population Management Strategies

Refugia, large areas that are not trapped and free from land-use impacts, can serve as sources of dispersing individuals and have been shown to be effective at ensuring the persistence and recovery of fisher and American marten populations (deVos 1951; Coulter 1960). The persistence of wolverine populations in Montana, despite years of unlimited trapping and hunting, was attributed solely to the presence of designated wilderness and remote, inaccessible habitat (Hornocker and Hash 1981). Wolverines persisted in southwestern Alberta despite their extirpation elsewhere in the province, largely because of the presence of large refugia in the form of national parks.

Management Considerations

1. Wolverines occur at low densities, even under the most optimal conditions where they have been studied. This makes detection of wolverines and determination of the effects of management activites on them difficult.

2. Reproductive rates are low and sexual maturity delayed, even in comparison with other mammalian carnivores.

3. Trapping accounts for a high proportion of wolverine mortality, affecting even populations that are locally protected.

4. Transient wolverines likely play a key role in the maintenance of spatial organization and the colonization of vacant habitat. Factors that affect movements by transients may be important to population and distributional dynamics.

5. If an objective is to have wolverines colonize an area through dispersal, then trapping of the source

Table 4.--Estimated densities of wolverine populations in North America, by location. Densities are expressed as a range when more than one estimate was available.

Density (km^2/wolverine)	Location	Method of calculation	Reference
North Slope of Alaska			
48-139[1]	NW Alaska	Telemetry, mean home range size	Magoun 1985
Central Yukon			
409-778	NC Yukon	Habitat suitability rating[2]	Banci 1987
Northern Boreal Forest (Yukon and British Columbia)			
37-656	SC Yukon	Habitat suitability rating[2]	Band 1987
177	SW Yukon	Telemetry, mean home range size	
Alaska Range			
209	SC Alaska	Logarithmic extrapolation[3]	Whitman and Ballard 1983
185, 213	SC Alaska	Aerial estimator[4]	Becker and Gardner 1992
Taiga Plains of Northwest Territory			
210	NE British Columbia	Harvests, Snow-tracking	Quick 1953
Northern Rocky Mountain Forest			
65[5]	NW Montana	Telemetry, mean home range size, snow-tracking	Hornocker and Hash 1981
150-200	NW Montana	Estimated, fringe areas to core study area	Hash 1987

[1] Resident fall population, including adults, sub-adult daughters that settled next to natal area, and kits.
[2] Density for one ecoregion determined from an intensive field study. Habitat capability of other ecoregions extrapolated from relationship between trapper success and density.
[3] Includes kits but not sub-adults; assumes that male home ranges average 627 km^2.
[4] Furbearer estimation technique based on probability sampling (Becker and Gardner 1992).
[5] May have included juveniles.

population, even if it is some distance away, may interfere with this objective. Because wolverines are wide-ranging, conservation programs need to transcend jurisdictional boundaries.

6. Harvest data can be used to monitor wolverine populations.

7. Refugia may be the best means of ensuring persistence of wolverine populations. Because wolverines are wide-ranging, refugia must be very large. Areas assigned permanently to one trapper can serve as refugia when pelt prices and trapping effort are low, which is the current situation in most of western North America. However, for refuges to be effective in population maintenance, they must not be harvested regardless of pelt prices.

Research Needs

1. Investigate the proportion of females that are pregnant in the wild, the proportion of kits that survive to weaning, and the factors that limit reproductive success. Knowing how reproductive success varies with environmental factors such as food availability, female condition, and the availability of natal dens will help in predicting population growth rates.

2. Use population models to understand the dynamics of wolverine populations and to determine the sustainability of harvests. Field studies are needed to increase the data base on population attributes and to parameterize these models. Mathematical modeling can also help to direct future research.

3. Invesigate the utility of remote cameras as a means of detecting wolverines or indexing their numbers.

4. Determine the cumulative impacts of trapping and timber harvesting on wolverine populations.

REPRODUCTIVE BIOLOGY

Mating Behavior

Wolverines have bred in captivity during May (Mehrer 1976) and July (Mohr 1938) and in the wild during June (Krott and Gardner 1985) and August

(Magoun and Valkenburg 1983). All adults, even females with dependent kits, appear to breed. Females may take longer to become estrous in their first breeding season and females that are not raising kits may come into breeding condition earlier than females with kits (Magoun 1985). The implication of a staggered entry into estrus by females is that males, which must travel extensively to monitor the breeding condition of females, have a better chance of encountering estrous females than if all females were in estrus synchronously. A long breeding season and prolonged estrus improve these chances further.

Breeding of wolverines in the wild in Alaska was described by Magoun and Valkenburg (1983) and Krott and Gardner (1985). Breeding pairs of wolverines restrict their movements and stay together, usually within a few meters, for 2-3 days (Magoun and Valkenburg 1983), suggesting that they copulate repeatedly. Induced ovulation has been shown for other mustelids and likely also occurs in the wolverine, necessitating prolonged intromission.

Natal Dens

Information on the use of natal dens in which the kits are born by wolverines in North America is biased to tundra regions where dens are easily located and observed. These natal dens typically consist of snow tunnels up to 60 m in length (Pulliainen 1968; Magoun 1985; Roskaft 1990). Bedding does not appear necessary, inasmuch as kits were found in shallow pits dug on the ground (Pulliainen 1968). Snow tunnels in northwest Alaska were also used by lone wolverines (Magoun 1985), suggesting that they dig tunnels or use existing tunnels as resting sites as well.

Natal dens above treeline appear to require snow 1-3 m deep (Pulliainen 1968) that persists into spring. In Finland, Pulliainen (1968) believed that dens that wolverine had dug themselves were preferred, because caves were rarely used, although available. Little is known of the distribution of den sites in the landscape. The proximity of rocky areas, such as talus slopes or boulder fields, for use as dens or rendezvous sites was important for wolverines in Norway (Roskaft 1990), in the Soviet Union (Ognev 1935), and in Idaho (unpublished data in Copeland 1993). Natal dens may be located near abundant food, such as cached carcasses or live prey (Haglund 1966; Rausch and Pearson 1972; Youngman 1975).

Females with young in Arctic Alaska spend much of their time in natal dens during March and April (Magoun 1985). Dens are abandoned in late April or early May, because of snowmelt (Magoun 1985; Pulliainen 1968). While the kits are too young to travel, the female hunts alone after leaving the kits at rendezvous sites (Magoun 1985). These rendezvous sites usually were portions of snow tunnels remaining from winter or remnant snowdrifts (Magoun 1985). Two other rendezvous sites included a rock cave and a boulder-strewn hilltop with no large snowdrifts (Magoun 1985).

Limited information is available on dens in forested habitat. In northern Lapland, most of the dens in forests were associated with spruce (*Picea* sp.) trees; five consisted of holes dug under fallen spruces, two were in standing spruces, and one natal den was inside a decayed, hollow spruce (Pulliainen 1968). Ognev (1935) reported that dens in Kamchatka were usually constructed in the "hollows" (cavities) of large trees. Rarely, kits have been found relatively unprotected, on branches and on the bare ground (Myrberget 1968). If females are disturbed they will move their kits, often to what appear to be unsuitable den sites (Pulliainen 1968).

Pulliainen (1968) hypothesized that one of the factors affecting the selection of a natal den site was the ease with which it could be adapted to a den. Seton (1929) reported dens in abandoned beaver lodges (as did Rausch and Pearson 1972), old bear dens, creek beds, under fallen logs, under the roots of upturned trees, or among boulders and rock ledges. In Siberia, dens were found in caves, under boulders and tree roots, and in accumulations of woody debris consisting of broken or rotted logs and dry twigs (Stroganov 1969). Natal dens in Montana were most commonly associated with snow-covered tree roots, log jams, or rocks and boulders (Hash 1987).

Management Considerations

1. Where wolverines occupy alpine areas in summer, the impact of human recreation on mating pairs and on family groups needs to be considered. Regulations that maintain the wilderness quality of an area, such as management of access, will help to minimize possible impacts on breeding wolverines and on females with kits.

2. Den sites in forested areas described to date in forested areas suggest that physical structure may be important for denning. Low availabilty of natal dens may limit reproduction in some areas, especially

those that have been extensively modified by logging or other land-use practices.

3. The distribution of natal den and rendezvous sites in the landscape, with respect to the distribution of food sources and security cover, may impact kit survival. In tundra habitats, deep snow drifts, such as in ravines, appear to be important.

4. Habitats that provide the appropriate structures, such as large cavities, coarse woody debris, and old beaver lodges, likely will provide den sites. Information is not available on the numbers of natal or maternal dens or rendezvous sites required.

Research Needs

1. Investigate factors important in the selection of natal and maternal dens, especially in forested habitats. Determine how the structure and distribution of natal dens and rendezvous sites contribute to kit survival.

2. Determine how the distribution and abundance of predators such as cougars, bears, and raptors affect the location and types of natal dens and rendezvous sites used by wolverines.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Wolverines are generally described as opportunistic omnivores in summer and primarily scavengers in winter. Winter diets have been determined from gut contents and scats and mostly reflect northern areas: the Yukon, Alaska, and the Northwest Territories. In the southern part of the wolverine's geographic range, quantitative diet data are available only for Montana.

Diets

The frequency of occurrence of prey remains does not necessarily indicate importance, because the size of prey and the amounts consumed affect their appearance in scats and gastro-intestinal tracts. Also, scavenging species tend to feed on animal remains, which tend to be bones and fur. This can overestimate the importance of scavenged foods relative to animals (e.g., snowshoe hare [*Lepus americanus*]) consumed in their entirety. Still, scats and gastrointestinal tract contents likely reflect annual and seasonal differences in food availability.

All studies have shown the paramount importance of large mammal carrion (table 5), and the availability of large mammals underlies the distribution, survival, and reproductive success of wolverines. Over most of their range, ungulates provide this carrion, although in coastal areas, marine mammals may be used. Wolverines are too large to survive on only small prey.

Large mammals are important all year (table 5), although carrion tends to be more available at some seasons than others. Ungulate carrion from natural mortalities and kills by humans is most available in fall and winter. For barren-ground caribou, adults dying during migration and calves dying at or just after birth become available in spring. In the coastal Arctic in the spring, wolverines prey on seal pups on sea ice (Anne Gunn, pers. comm.) and in some coastal Alaskan areas, sea mammal carcasses provide abundant carrion (LeReseche and Hinman 1973).

North of the boreal forest, barren-ground caribou are the most important source of ungulate carrion (table 5). Novikov (1956) thought some Old World wolverines migrated to follow reindeer (*Rangifer rangifer*), their primary winter food. Such a migration was also hypothesized by Kelsall (1981) for Canada because of the numbers of wolverine taken during predator control on occupied caribou ranges in winter (Kelsall 1968). Research has not shown wolverines to migrate, although they associate closely with caribou in the North. Moose are consumed where available (Kelsall 1981). The distribution of wolverines in northern Saskatchewan has closely followed the changes in distribution of the barren-ground caribou (W. Runge, pers. comm.). This may also be true in Alberta and Manitoba. The decline of the wolverine in Labrador coincided with the decline of caribou (Banfield and Tener 1958) and recent sightings of wolverines in Labrador have coincided with expansions of caribou range (Banci 1987).

South of the tundra, ungulates gain importance according to their availability. In the Yukon Forest and Northern Boreal Forest ecoprovinces of central Alaska and the Yukon, both moose and caribou are common (table 5). Where they occur, Dall sheep (*Ovis dalli*) and mountain goat (*Oreamnos americanus*) are eaten, but less so than moose or caribou, perhaps because the precipitous terrain occupied by sheep and goats reduce their accessibility (Banci 1987). Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) were the primary ungulates in the diet of wolverines in Montana (table 5, Hornocker and Hash 1981).

Bone and hide may be important foods. They may be available for several months after an ungulate dies (Haynes 1982). Wolverines in northwest Alaska and in the Yukon at times consumed only bone (Magoun 1985; Banci 1987). The presence of bone and fur in the diet (table 5) emphasizes the use that wolverine make of old kill sites, and the general scarcity of food. The large numbers of wolverines with empty gastro-intestinal tracts in food habits studies (table 5) is evidence of the uncertainty in the availability of food.

Table 5.-Diets of wolverine in North American ecoprovinces.

	Percent frequency of occurrence[1]						
Prey Item	**Northern Boreal Forest (Yukon & British Columbia)**	**North Slope of Alaska**	**Central Alaska**			**Northern Territories**	**Northwest Rocky Mountains**
Winter							
Snowshoe hare	27		6	[2]	45	13	16
Porcupine	16		3	15		2	4
Sciuridae	14	40	9			2	11
Aves	12	11	11	[2]	6	12	6
Small mammals	10	30	20	[2]	16	2	6
Beaver/muskrat	<1			3		4	2
Carrion							
caribou	8	37	20	60[3]		53	80
moose	14		25			33	3
other	7[4]						27[5]
unidentified	23			6			45[5]
fat/flesh	16				12		
bone	32						
Fish	5				6	14	
Other	4	18	20		2	5	18
Empty/trap debris	31				73	39	
Reference[7]	a)	b)	c)	d)	e)	f)	g)
Snow-Free Periods							
Ungulate	7, 30[8]	12[8]	33[9]				
Ground squirrel	0, 17	40	33				
Aves[10]	7, 14	2	11				
Mice & voles[11]	93, 57	12	11				
Beaver			11				
Marmot	7, 0						
Reference[12]	a), b)	c)	d)				

[1] Percent frequency Is based on the occurrence of each prey of the total number of scats or gastro-intestinal (g.i.) tracts. Empty g.i. tracts were not used In calculations of percent occurrence for prey items.

[2] Proportion not reported but rare,

[3] Undifferentiated between moose and caribou.

[4] Bovids.

[5] Deer or elk.

[6] Domestic cow and horse.

[7] a) Banci 1987, Yukon; n=411 gastro-intestinal tracts. November-March, 1982/83-1984/85. 126 g.i. tracts were empty or contained only vegetation or only wolverine hair.

b) Magoun 1985, Alaska; n=82 scats, November, February, March, 1979-1980.

c) Gardner 1985, Alaska; n= 35 colons only, December-March 1979-1982.

d) Rausch 1959, Alaska; n=20 stomachs.

e) Rausch and Pearson 1972, Alaska; n=192 gastro-intestinal tracts, winter. Only 51 g.i. tracts with prey items.

f) Poole 1991-1992, Northwest Territories; n=173 stomachs, winter 1987/88-1991/1992.

g) Hornocker and Hash 1981, Montana; n= 56 scats, 5 winters December 1972 April 1977.

[8] Caribou.

[9] Moose.

[10] North Slope; ptarmigan.

[11] Microtus sp., Lemmus sp., Phenacomys sp., Clethrionomys sp.

[12] a) Newell 1978; 15 scats collected on trails,

b) Newell 1978; 30 kit scats collected from 2 natal dens.

c) Magoun 1985; n=48 observations of 362 5-minute observation periods, May-August, 1978-1981.

d) Gardner 1985; n=9 aerial observations; April-mid-October, during 70 telemetry flights, 1980-1982.

Small mammals are primary prey only when carrion of larger mammals is unavailable (Banci 1987).

Snowshoe hares, at both high and low population levels, were important in the diets of wolverines in the Yukon (Banci 1987, table 5) and Alaska (Rausch and Pearson 1972). I expect that, especially during hare population lows, habitats that maintain pockets of them (Hatler 1988) will be important foraging areas for wolverines. In western North America, there is a general decrease in abundance and in the amplitude of population fluctuations of snowshoe hares with decreasing latitude (Hatler 1988). Hares likely are less important in the wolverine diet in these areas.

Porcupines (*Erethizon dorsatum*) occur in wolverine diets in Alaska, the Yukon, and Montana (table 5). Although they represent a large meal, porcupines appear to be limited to those wolverines that have learned to kill them (Banci 1987). The frequency of red squirrels (*Tamiasciuris hudsonicus*) in wolverine diets in northern forested habitats (Gardner 1985; Banci 1987) is a reflection of their wide distribution and availability throughout winter. Arctic ground squirrels (*Spermophilus parryi*) composed 26% of all sciurids in the winter diet of Yukon wolverines (Banci 1987) and the majority of the diet in northwest Alaska, where snowshoe hares were absent (Magoun 1985). Wolverines cache hibernating sciurids such as ground squirrels and hoary marmots (*Marmota caligata*) in the snow-free months for later use and excavate them from winter burrows (Gardner 1985; Magoun 1985).

Birds occur in the diet according to their availability. Wolverine prey on ptarmigan (*Lagopus* spp.) in winter in the Yukon (Banci 1987), Alaska (Gardner 1985; Magoun 1985), and the Northwest Territories (Boles 1977). Prey that occur sporadically in diets, such as American marten, weasel (*Mustela* spp.), mink (*M. vison*), lynx, and beaver (*Castor canadensis*), likely are mostly scavenged. Vegetation is consumed incidentally although ungulate rumens and may contain nutrients that wolverines cannot obtain from other foods (Banci 1987).

Some foods may be abundant and predictable--for example, spawned salmon frozen in river ice (Banci 1987). Other abundant food sources likely include spawning salmon in the fall and intertidal areas of the Pacific coast. Such areas may support high densities of wolverines (Banci 1987).

Seasonal Variation in Diets

Although data are limited, in general, diets during snow-free periods are more varied than in winter because of the greater availability and diversity of foods, such as berries, small mammals, sciurids, and insect larvae (table 5). Berries can be important in fall (Bausch and Pearson 1972) and during late winter and spring. Wolverine in southwest Yukon ate kinnikinnick (*Arctostaphylos uva-ursi*) berries that were high in carbohydrates because of freezing and thawing (Banci 1987).

Spring and summer may be the only seasons when sexual differences in diet may occur. The movements of females with kits are restricted at these times and their diets may differ from males that are not so restricted. Diet does not appear to differ by age, at least in winter (Banci 1987). Success at foraging may differ between juveniles and adults because of differences in experience, but this has not been shown.

Foraging Behavior

Although mostly scavengers, wolverines can prey on ungulates under some conditions. Because of their low foot loads (pressure applied to substrate) of 22 g/cm^2 (Knorre 1959), wolverines can prey on larger mammals in deep snow and when ungulates are vulnerable. Grinnell (1920, 1926) described wolverines killing moose, caribou, and elk. Guiget (1951) described an unsuccessful attack of a wolverine on a mountain goat and Burkholder (1962) a successful attack on a caribou bull. Gill (unpublished data 1978) described a wolverine killing a young female Dall sheep hindered by snow in the Northwest Territories. Teplov (1955) described instances in which pregnant cow moose aborted when chased by wolverines and the wolverines ate the aborted fetuses. A similar case with a wolverine and a caribou cow was observed in the Yukon (P. Temple, pers. comm.).

Caching of food by wolverines has been described by most studies except that in Montana. The frequency of caching by wolverines may be affected in various ways by the presence of other carnivores (Hornocker and Hash 1981; Magoun 1985).

Management Considerations

1. Activities that increase availability of foods generally will affect wolverines positively, whereas those that reduce prey populations will do so negatively. The close relationship between wolverines and large mammals implies that activities that decrease large mammal populations will negatively impact wolver-

ine. These activities could include wolf predation, excessive harvesting by humans and human-caused losses of ungulate winter ranges. Some ungulate species may be enhanced by the provision of early seral stages through logging or burning. However, these and other land-use activities may exclude wolverines from areas that ungulates still use if these habitats do not provide for the wolverine's other life needs.

2. Because young wolverines mature rapidly, the availability and distribution of food during the snow-free season may determine the survival of females with kits.

Research Needs

1. Investigate wolverine diets in the southern part of the geographic range. This will improve understanding of the variation in diets over the geographic range and of the importance of foraging habitats.

2. Investigate and compare diets of females with kits to lone females and males.

3. Study caching behavior by wolverine. If the types of caches used are a function of habitat type, they may be impacted by land-use activities and their absence may negatively impact wolverine survival.

HABITAT RELATIONSHIPS

Broadly, wolverines are restricted to boreal forests, tundra, and western mountains. The vegetation zones (Crowley 1967; Rowe 1972; Hunt 1974; Bailey 1980; Allen 1987) occupied by wolverines include the Arctic Tundra, Subarctic-Alpine Tundra, Boreal Forest, Northeast Mixed Forest, Redwood Forest, and Coniferous Forest. They are absent from all other vegetation zones, including the prairie, deciduous, and mixed forests of eastern North America; California grassland-chaparral; and sagebrush and creosote scrublands.

Researchers have generally agreed that wolverine "habitat is probably best defined in terms of adequate year-round food supplies in large, sparsely inhabited wilderness areas, rather than in terms of particular types of topography or plant associations" (Kelsall 1981). Although this is generally true at the landscape scale, stand-level habitat use by wolverines in forests has not been adequately investigated. Results from northern studies (Gardner 1985; Banci 1987) cannot be extrapolated to the southern part of the range, nor can the one study in the Northern Rocky Mountain Forest of Montana (Hornocker and Hash 1981) be considered representative of that ecoprovince.

Habitat Use

Landscape scale

In British Columbia, the highest harvests of wolverines per unit area and effort occur in the Shining Mountains and Northern Boreal Forest ecoprovinces. The combination of very wet mountains and very dry rainshadow valleys provides the Shining Mountains with a high diversity and abundance of large mammals, including mountain goats, mule and white-tailed deer, elk, bighorn sheep (*Ovis canadensis*), and woodland caribou (Demarchi et al. 1990). Predators such as grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolves, and cougars also are common, at least in the Canadian part of the ecoprovince. The best habitat for wolverines in the Yukon (Banci 1987) is in the Northern Boreal Forest. This ecoprovince is characterized by mountains and plateaus separated by wide valleys and lowlands, with extensive subalpine and alpine habitats (Demarchi et al. 1990). Ungulates and predators are abundant here as well.

I expect that the lowest densities of wolverines occur in the ecoprovinces that have the lowest habitat diversity and prey abundance-the Boreal Shield and the Boreal Plains ecodivisions. These ecodivisions are among the first where wolverine disappeared with the advance of civilization.

Stand level

Preferences for some forest cover types, aspects, slopes, or elevations have been primarily attributed to a greater abundance of food (Gardner 1985; Banci 1987), but also to avoidance of high temperatures and of humans (Hornocker and Hash 1981). The greater use of subalpine coniferous habitats by males in southwest Yukon in winter was speculated to be due to higher densities of ungulate kills in these habitats (Banci 1987). Similarly, the use of alpine areas in south-central Alaska in summer was attributed to the arctic ground squirrels there (Whitman et al. 1986). In Montana, Hornocker and Hash (1981) believed that wolverines used higher ranges during the snow-free season because they were avoiding high temperatures and human recreational activity (Hornocker and Hash 1981).

Predation may influence wolverine habitat use, depending on the predator complement in the envi-

ronment, including humans. In south-central Alaska, wolverine use of rock outcrops was greater than the availability of those areas during summer (Gardner 1985), perhaps because rock outcrops were being used as escape cover from aircraft. However, wolverines may have also been hunting marmots and collared pikas (*Ochotona collaris*) (Gardner 1985). Wolverines may climb trees to escape wolves (Boles 1977, Grinnell 1921), although if the trees are not high enough, such attempts may be unsuccessful (Burkholder 1962). Wolverines are found in a variety of habitats and do not appear to shun open areas where wolves are present. Wolverines occur locally with cougars, especially in British Columbia and the northwestern United States. Trees would not be an effective defense because cougars are adept at climbing. It is likely that wolverines use various habitat components, such as rock outcrops or trees, for escape when they feel threatened.

Aside from anecdotal reports, only Hornocker and Hash (1981) have reported on the use of resting sites by wolverines in forested habitats. Overhead cover may be important for resting sites as well as natal and maternal dens. Resting sites in Montana were often in snow in timber types that afforded cover (Hornocker and Hash 1981).

Impacts of Land-Use Activities

The impacts of land-use activities on wolverine habitat are likely similar to those that have been described for grizzly bears, another species that has been negatively impacted by land-use activities. Agriculture, domestic cattle ranges and grazing, forestry, mineral and petroleum exploration and development, hydroelectric power development, human settlement, population growth, and recreation all have affected the productivity and integrity of habitat within wolverine range (Banci et al., in press). Habitat alterations have been limited in northern ecoprovinces but have been extensive in the northwest United States, southern British Columbia and Alberta.

The greatest impacts on the potential of the land to support wolverines in Canada have occurred in the Boreal Plains ecodivision because of extensive agricultural development; in the Pacific Northwest Coast and Mountains because of forestry, settlement, and access; in the Central British Columbia Plateaus because of losses of productive riparian areas and wetlands, and predator removal because of conflicts with agriculture; and in the Shining Mountains because of water impoundments and highway construction (Banci et al., in press). Impacts of habitat loss and fragmentation have been large in all ecoprovinces in the northwestern United States, except for those areas in parks or other refugia.

The impacts of logging and associated activities on wolverines and wolverine habitat can only be surmised. A preference by wolverines for mature to intermediate forest in Montana (Hornocker and Hash 1981) was not apparent in southwest Yukon (Banci 1987) or in south-central Alaska (Gardner 1985). Hornocker and Hash (1981) reported that although wolverines in Montana occasionally crossed clearcuts, they usually crossed in straight lines and at a running gait, as compared to more leisurely and meandering patterns in forested areas. The study area in Montana was the only one a portion of which had been logged (Hornocker and Hash 1981). However, no differences in movements, habitat use, or behavior was noted between wolverines occupying the half of the area that was logged and the half that had not (Hornocker and Hash 1981).

Wolverine populations that have been or are now on the edge of extirpation have been relegated to the last available habitat that has not been developed, extensively modified, or accessed by humans (such as roads and trails). On Vancouver Island, wolverines survive mainly in habitats that are largely inaccessible, the central mountain ranges and the west coast, in contrast to an historical distribution that ranged from coast to coast. They have largely been maintained in western Alberta by the extensive system of national parks. In Montana, the persistence of wolverine despite years of unlimited hunting and trapping has been attributed to the presence of large, isolated wilderness refugia: Glacier National Park and the Bob Marshall Wilderness (Hornocker and Hash 1981). In Washington and Oregon, wolverine reports come from the largely protected North Cascades. Similarly in Idaho, Wyoming, and Colorado, wolverines generally are sighted in remote and mountainous areas. The perception that wolverines are a high-elevation species has arisen because where wolverine are surrounded by people, they are usually found in the most inaccessible habitats, the mountain ranges.

Some wolverines tolerate civilization to the extent of scavenging at dumps in northern communities and living adjacent to urban areas in the north (LeResche and Hinman 1973; Holbrow 1976). They use food and garbage at trapper cabins and mines and have fol-

lowed traplines, systematically removing furbearers from traps. This is opportunistic foraging behavior, inasmuch as there is no evidence that human food sources are used extensively or that wolverines become habituated to human food, except for those that are starving. The presence of humans may conflict directly with wolverines. Hornocker and Hash (1981) suggested that human access on snowmobiles or all-terrain vehicles in winter and early spring could cause behavioral disturbances.

Wolverines seem to have been most affected by activities that fragment and supplant habitat, such as human settlement, extensive logging, oil and gas development, mining, recreational developments, and the accompanying access. Despite their association with remote and generally wild habitats, information is insufficient to define what wilderness components wolverines require or to gauge when the impacts of a land-use activity have been excessive.

Management Considerations

1. With our current dearth of knowlege, conserving wolverine populations may require large refugia, representative of the vegetation zones that wolverine occupy and connected by adequate travel corridors. Refugia have a dual purpose, also serving as a source of dispersing wolverine for other areas. Appropriate refuge sizes are unknown but will depend on habitat suitability. The lower the wolverine density, the larger the refuge necessary. It is best to think of refuge size in terms of wolverine reproductive units, 1 male and 2-6 females. How many reproductive units in a refuge are necessary to ensure population maintenance and dispersal? If population characteristics such as density and recruitment are known, modeling can help to answer this question.

2. The dispersal and travel corridors that connect refugia, at least for males, likely need not have the habitat attributes necessary to support self-sustaining populations. Atypical or low quality habitats may be important to wolverines if they connect otherwise isolated populations and allow for genetic exchange or colonization. Because females establish home ranges next to their natal area and their dispersal distances are less than for males, requirements for dispersal corridors may be more specialized. The biggest limiting factor in recolonization likely is the dispersal of young females.

3. Because refugia for wolverines will no doubt be very large, the species will benefit by being part of a large carnivore conservation strategy in which connected refugia are established for grizzly bears, wolves, cougars, and wolverines. Such a strategy will help to ensure that the entire range of wolverine habitat needs will be accommodated and lessens the chance that refugia will not be large enough or that an important requirement will not be adequately met.

4. Until more information becomes available, habitat management prescriptions that successfully provide for the life needs of species such as the American marten, fisher, and lynx and their prey will also provide for the needs of wolverine at the stand level. However, it is not known whether this will provide for wolverine habitat needs at the landscape or larger scales.

Research Needs

1. Study the habitat needs of wolverine in forests, because there is no sound basis for developing habitat management prescriptions at the stand level. Information that will allow development of recommendations for road densities, sizes of areas on which timber is cut, minimum cover requirements, natal dens, resting sites, and coarse woody debris is required.

2. Remote censusing devices such as cameras may be useful to determine the use of habitats by wolverine and to address the impacts of forest harvesting.

3. To determine appropriate refuge locations and sizes and travel corridors for wolverines, their current distribution at both small and large map scales, with current and projected land-use activities, must be mapped. This process will also assist in identifying habitats that have been fragmented and isolated and populations that are isolated. In line with the recommendation to consider the wolverine as part of a large carnivore conservation strategy, much of this work in the conterminous United States can be coordinated with that occurring for grizzly bear ecosystems.

4. If the dispersal of young females is the primary limiting factor in the recolonization of denuded habitats, providing for their dispersal needs will be important in recovery efforts. Information on the movements of dispersing females and their use of habitats is necessary to ascertain the appropriate composition and location of travel corridors.

5. Consideration of wolverine habitat needs in managed forests is complex because wolverines use habitats at different scales. Research is needed on what it means for wolverine to use habitats at the landscape scale and how this can be translated into habitat management guidelines. Attributes that may

be important at the landscape scale are the percentage of different seral stages; shape, placement and numbers of timber cuts; the time between cuts; and locations of travel corridors. Criteria for recreational developments such as ski areas, hiking trails, and snowmobile and all-terrain vehicle use also need to be developed at the landscape scale.

HOME RANGE

Home ranges of adult wolverine in North America range from less than 100 km^2 to over 900 km^2 (table 6). The variation in home range sizes among studies partly may be related to differences in the abundance and distribution of food. Wolverines in the southwest Yukon and in southcentral Alaska concentrated their use at large ungulate carcasses (Gardner 1985; Banci 1987) and locations of spawned salmon (Banci 1987). Localized areas of high food availability were cited as the reason for small home ranges in southwest Yukon (Banci and Harestad 1990). In northwest Alaska, food levels were particularly low and dispersed because of the absence of overwintering caribou and home ranges of wolverine were larger than all others reported (Magoun 1985).

The presence of young restricts movements and home range size of females (table 6). Yearly home ranges for a female with young was 47 km^2 (discounting 2 long-distance movements) in southwest Yukon (Banci and Harestad 1990); 100 km^2 each for 2 females in Montana (Hornocker and Hash 1981); a mean of 105 km^2 in south-central Alaska (Whitman et al. 1986); and a mean of 70 km^2 in northwest Alaska (Magoun 1985). Male home ranges are typically larger than those of females (table 6). Spring and summer home ranges of adult males, but not adult females, increased during the breeding season in Alaska and Montana (Hornocker and Hash 1981; Gardner 1985; Magoun 1985) but not in the Yukon (Banci and Harestad 1990). In the latter, localized and abundant food may have been responsible for females being readily available to the adult male, making extensive breeding movements unnecessary (Banci and Harestad 1990).

This pattern of home range use is consistent with a carnivore spatial strategy in which the spacing of females underlies the distribution of males, at least

Table 6.--Annual home ranges (km^2) of wolverine in North America.

Location	Mean	Range	*n*	Reference
Adult males				
Northwest Alaska	666	488-917	4	Magoun 1985
Southcentral Alaska	637		1	Gardner 1985
Southcentral Alaska	535		4	Whitman et al. 1986[1]
Southwest Yukon	238		1	Banci 1987
Montana	422		9	Hornocker and Hash 1981
Subadult males				
Southwest Yukon	526		1	Banci 1987
Idaho	435		1	Copeland 1993[2]
Adult females with young				
Southwest Yukon	139[3]		1	Banci 1987
Southcentral Alaska	105[4]		3	Whitman et al. 1986
Northwest Alaska	73	55-99	3	Magoun 1985
Montana	100		2	Hornocker and Hash 1991
Adult females without young				
Northwest Alaska	126	56-232	6	Magoun 1985
Southwest Yukon	272	202-343[5]	2	Banci 1987
Montana	388	963 (max.)	11	Hornocker and Hash 1981
Idaho	338	160-516[6]	2	Copeland 1993

[1] Estimated using the relationship between time of monitoring and home range size.
[2] 90% minimum polygon home range is 369 km^2.
[3] If two long-distance movements are excluded, home range is 47 km^2.
[4] Estimated using the relationship between time of monitoring and home range size.
[5] If I long-distance movement is excluded for each female, home ranges are 153 and 157 km^2, with a mean of 155 km^2.
[6] 90% minimum polygon home ranges are 82 and 447 km^2; core harmonic mean ranges are 79 and 306 km^2.

in the breeding season, but food underlies the distribution of females (Sandell 1989). Home ranges of females should reflect the minimum size necessary to obtain food more than those of males (Sandell 1989). Consistent with this prediction, wolverine females typically cover their home ranges uniformly, unless they have kits and concentrate their movements at natal dens or rendezvous sites (Gardner 1985; Hornocker and Hash 1981). Males, instead, typically have one or more foci of activity within the home range (Hornocker and Hash 1981; Gardner 1985).

Winter home ranges typically overlap with those used in the snow-free season but also include different habitats, even if there are no significant differences in the size of seasonal home ranges (Hornocker and Hash 1981; Magoun 1985; Banci 1987). Differences between seasonal home ranges can be attributed to changes in prey distribution and availability. Wolverines of both sexes appear to maintain their home ranges within the same area between years (Magoun 1985; Banci 1987). There may be slight changes in the yearly boundaries of home ranges with the addition of juvenile females adjacent to the natal area, with mortality, and with immigration. For example, when a resident dies, a neighbor may assume part of the vacant home range (Magoun 1985; Banci 1987).

Home ranges of subadults, especially males (table 6), are transitory areas used before dispersal. Typically, home range use by immature males is characterized by extensive movements out of the natal home range (Gardner 1985; Magoun 1985; Banci 1987). Adults may make temporary long-distance movements outside the usual home range, which are apparently not related to dispersal. Adult females in Yukon made one or two long-distance movements in summer only, inflating the size of their annual home ranges if these movements were included (table 6). Such excursions were also observed frequently for both sexes in Montana (Hornocker and Hash 1981) and were documented for females in northwest Alaska (Magoun 1985).

Spatial Patterns

The basic spatial pattern in Mustelidae has been described as intrasexual territoriality, in which only home ranges of opposite sexes overlap (Powell 1979). In general, spatial patterns in wolverines are consistent with this, although partial overlap of home ranges of some wolverines of the same sex is common. In northwest Alaska, home ranges of adult males were exclusive in winter, whereas those of adult females overlapped only in winter (Magoun 1985). In southwest Yukon, spatial but not temporal overlap of adult female home ranges occurred during winter (Band and Harestad 1990). It is likely that neighboring adult females are related, resulting in a greater tolerance for overlap between individuals (Magoun 1985). Home ranges of adult males and females overlap extensively, with the range of one male covering the ranges of 2 to 6 females (Magoun 1985; Banci 1987). Also, adult home ranges overlap with those of immatures (unpublished data in Whitman and Ballard 1983; Magoun 1985; Banci and Harestad 1990). Preliminary data for Idaho is consistent with this pattern, with overlap occurring only between juveniles and adults and between sexes (unpublished data in Copeland 1993).

In northwest Montana, Hornocker and Hash (1981) attributed the extensive overlap of wolverine home ranges of both sexes and all ages to the effects of human predation, which removed individuals before they established tenure, contributing to behavioral instability. This study was conducted from 1972 to 1977 and until 1975, the wolverine in Montana was classified as a predator and unlimited killing was permitted (Hornocker and Hash 1981). It was not until the last 3 years of their study that trapping was prohibited in their study area. Considering that Montana had only recently been recolonized by wolverine, it is possible that the individuals that were studied were not able to establish home ranges. Hornocker and Hash (1981) could not ascertain whether individuals were transients or residents. It would be interesting to know if now, almost 20 years after protection, adult wolverine have established intrasexual territories.

At abundant and concentrated sources of food, such as large carrion or accumulations of spawned salmon, tolerance among adult wolverines appears to increase and adult individuals of the same sex may feed concurrently at the same site, or at the same food source (Banci 1987). It is unlikely that the dominance structure normally present in areas that do not have such foods breaks down. Rather, the individual home range boundaries of wolverines should shrink if it is not possible or profitable for them to defend an abundant food source, consistent with Lockie's (1966) prediction that individual home ranges will vary in exclusiveness depending on the concentration of resources in different seasons or habitats.

Communication

Wolverines have complex structures that may be important for chemical communication, including anal glands, a possible abdominal gland (Hall 1926), and plantar glands on the rear feet (Buskirk et al. 1986). The morphology of these structures has not been well studied. Wolverines also mark by urinating, defecating, scratching the ground, and biting trees (Koehler et al. 1980; Magoun 1985). Defecation does not appear to be an active form of scent marking although urination on older scats sometimes occurs, with these scats then acting as scent posts (Magoun 1985).

Urination appears to be the primary means of communication, often occurring at raised and traditional landmarks (Koehler et al. 1980; Magoun 1985). After urination, abdominal rubbing was the second-most used method of communication in captive wolverines (unpublished data in Long 1987). Marking with the anal glands appears to be primarily used as a fear or defense mechanism (Seton 1929; Krott 1960; Magoun 1985). Koehler et al. (1980) reported some of the few data on the use of musk in scent marking.

Wolverine devote considerable energy to scent marking, deviating from their line of travel specifically to mark objects (Koehler et al. 1980; Magoun 1985). As in other carnivore populations, scent marking in wolverines likely serves as a means of monitoring the reproductive status of individuals, assists in foraging, and maintains separation of individuals in space and in time (Gorman and Trowbridge 1989).

Management Considerations

1. Even within an ecoprovince, home range size and use by wolverine differ because of differences in habitats, in the distribution and availability of food, and in the intensity and extent of habitat alteration and other human influences. Home range sizes have been used to estimate densities in areas other than where they were determined, based on the assumption of intrasexual home range exclusivity. Because of the few data available, wolverine densities determined using home range size cannot be reliably extrapolated to the rest of an ecoprovince or used to compare ecoprovinces.

2. Localized and seasonally abundant sources of food such as carrion, salmon-spawning streams, and possibly berry patches are important to wolverines and receive heavy use within the home range. Land use activities may impact such habitats.

3. At the landscape level, the wolverine's large home ranges need to be considered in forest management planning. The area required by a wolverine reproductive unit, a male and 2-6 females, may be an important consideration in landscape planning.

Research Needs

1. Home range size and use that have been determined in or adjacent to remote undeveloped areas are biased to northern habitats and generally are not known for western forests. Opportunity is quickly eroding to determine wolverine home range and habitat use in western North American forests where habitats have not been modified and populations have not been heavily exploited. However, without such comparative information, the impacts of land-use practices such as forestry, intensive silviculture, and oil and gas exploration and development on wolverine home ranges and habitat cannot be assessed.

2. Scent marking is an important mechanism for communication. Field studies need to continue to examine the role of scent marking in population maintenance, both in established populations, and by transients and dispersers. This information can help in understanding how vacant habitats are colonized and how exclusive home ranges are established. Changes in marking behavior may also be the first evidence of the impacts of land-use practices, human activity, and habitat alterations on wolverine.

MOVEMENTS AND ACTIVITY

Wolverines can travel long distances in their daily hunting, 30-40 km being "normal" (Krott 1960; Haglund 1966; Pulliainen 1968). These distances, determined by snow-tracking, provide better estimates of the actual distances covered than does telemetry. In northwest Alaska, actual movements were 33% greater than straight line distances between telemetry locations (Magoun 1985).

Adult males generally cover greater distances than do adult females (Hornocker and Hash 1981; Gardner 1985; Magoun 1985) and may make longer and more direct movements (Hornocker and Hash 1981). During late winter, lactating females with young move less than solitary adult females (Gardner 1985; Magoun 1985). In May and June, hunting mothers periodically return to their young that have been left at rendezvous sites (Magoun 1985). In northwest Alaska, females returned to rendezvous sites at least

daily (Magoun 1985). Kits were moved to new rendezvous sites every 1-9 days and more frequently as they grew older (Magoun 1985). By June, kits were moved every 1-2 days (Magoun 1985). When her kits were 4-11 weeks old, a female in central Idaho used 18-20 den sites, moving her kits a total of about 26 km (unpublished data in Copeland 1993).

In the southwest Yukon, all 3 resident adult females made 1 or 2 long-distance movements of 11-31 km from their home range boundaries that lasted 1-2 weeks in summer (Banci 1987). In northwest Montana, wolverines of both sexes made frequent long movements out of their home ranges that lasted from a few to 30 days, and they always returned to the same area (Hornocker and Hash 1981). These long-distance movements appear to be temporary and not attempts to expand the home range. Whether these movements are exploratory or whether wolverine are returning to previously known feeding locations is unknown.

Except for females providing for kits or males seeking mates, movements of wolverine are generally motivated by food. Wolverines restrict their movements to feed on carrion or other high quality and abundant food sources (Gardner 1985; Banci 1987). In south-central Alaska, wolverines fed on ground squirrels in alpine areas in the spring and summer (Gardner 1985). In winter, they moved to lower elevations to feed primarily on wolf-killed and winter-killed moose and caribou (Whitman et al. 1986).

Dispersal

Young females typically establish residency next to or within the natal home range (Magoun 1985). Although some immature females disperse, males are more likely to do so. Male wolverines may disperse either as young-of-the-year or as subadults (Gardner 1985; Magoun 1985; Banci 1987). Dispersal can include extensive exploratory movements (Magoun 1985; Banci 1987). A subadult male left his home range of at least 7 months, stayed away for 2 months and then returned, remaining only 2 weeks (Banci 1987).

Magoun (1985) hypothesized that dispersal of young occurred as early as January and as late as May. The increased movements of young-of-the-year males, either exploratory or dispersal, make them susceptible to trapping as early as November (Banci 1987). The longest documented movement was 378 km by a male from southcentral Alaska to the Yukon over eight months (Gardner et al. 1986). Adult males appear to influence the dispersal and settlement of immature males (Banci 1987; Gardner 1985).

Rivers, lakes, mountain ranges, or other topographical features do not seem to block movements of wolverines (Banci 1987; Hornocker and Hash 1981). At times, wolverines will use rivers and streams as travel routes probably because prey species also use these travel routes (pers. obs.). Considering the wolverine's avoidance of human developments, extensive human settlement and major access routes may function as barriers to dispersal.

Management Considerations

1. In some areas, wolverines in alpine and subalpine habitats may be subjected to intense recreational activity in the spring and summer. This disturbance may impair kit survival if females are forced to use less secure den sites. Recreational activity may be a concern if den sites are limiting because wolverine have been relegated to high elevation areas due to extensive habitat loss and alteration. Access management plans may need to consider all-terrain vehicles, aircraft, and travel on foot and travel on horseback to protect denning females.

2. The long movements of wolverines suggest that recolonization of vacant habitats is not a concern. However, because of the tendency of young females to settle next to the natal area, recolonization may be delayed unless the source population has a high kit survival and young females are forced to disperse to find vacant habitats in which to establish home ranges. If dispersal is to be relied upon as a means of reestablishing populations, the productivity of the source population is important. Dispersal corridors that supply the requirements for young females are also important.

Research Needs

1. Dispersal distances of female wolverine may be considerably less than those of males. To predict the potential for success and length of time necessary for recolonization of vacant habitats, information is needed on the survival rate and distances dispersed by young females.

2. The long-distance movements made by adult resident wolverines appear to be rare enough that they have little impact on habitat or home range use. However, it is unlikely that a species would make such movements unless they conferred a positive benefit on survival. Future studies should attempt to document the nature of these movements, their occur-

rence over time, whether both sexes are involved, and whether factors outside the home range such as habitat, food availability, or other wolverine are influences.

COMMUNITY INTERACTIONS

Primarily scavengers, wolverine clean up after the more efficient hunter carnivores. They prey on species smaller than themselves, if abundant. Even where habitats are optimal, wolverines occur at such low densities that it is unlikely they have a major effect on numbers of any other species. They are not important food for any other species. As scavengers, they not only depend on carnivores like wolves, cougars, and bears, but conflict with them, occasionally being killed by them. Their most important predator is humans, through trapping and hunting. Likewise humans indirectly affect wolverines through prey, impacts on other carnivores, and habitat changes.

Wolverine and Prey

The presence of large mammals underlies the distribution and abundance of wolverines, especially in northern environments. North of treeline, the distribution of wolverines appears to be tied to that of the barren-ground caribou. Wolverines can survive for short periods if caribou are absent but may not reproduce during these times (Magoun 1985). Wolverine are too large to subsist solely on small prey. Nothing is known about the population dynamics of wolverines that have access to highly nutritional food sources, such as salmon in coastal and interior areas, intertidal habitats, and marine mammal carcasses. It is possible that locally productive wolverine populations have been lost in North America because of hydroelectric development and the subsequent loss of major salmon runs.

In the boreal ecoprovinces of western Canada and Alaska, the primary large mammal species for wolverine are caribou and moose. South of treeline, large mammal carrion is provided primarily by cervids, likely because their availability is greater than that of bovid species such as mountain goat and mountain sheep. In the Shining Mountains, Northern Rocky Mountain Forest, Pacific Northwest Coast and Mountains, and Sierra Nevada ecoprovinces, deer and elk are important. Although large carrion is a key element in the wolverine diet, the diet requires scavenging and hunting smaller prey. A prey base diverse in size and in species is important because large carrion is not always available. Snowshoe hares, especially, are important in diets from northern ecoprovinces. An abundance of large mammal carrion or a diverse prey base does not guarantee the presence of wolverines, especially if other life needs, such as denning habitat or travel corridors, are not met.

Wolverines, Wolves, and Humans

In their foraging activities, wolverine occasionally conflict with and may be killed by wolves, cougars, and bears. Predators are not likely to be a significant mortality factor on adult wolverines because they are killed only opportunistically, although predation on kits may occur.

Although few records were kept, wolverines likely were heavily impacted by the extensive wolf eradication programs carried out over much of North America early in this century. Private control efforts began shortly after the arrival of Europeans in the early 1600's (Stardom 1983) and government agencies took over in the 1950's and 1960's (Carbyn 1983). In Manitoba and the Northwest Territories, 1 wolverine was killed for each 8 to 9 wolves (van Zyll de Jong 1975; Kelsall 1968); an average of 1,800 wolves were killed yearly (Heard 1983). Trappers in the early 1900's also regarded wolverine as vermin because of their propensity to raid traplines and cabins, so trappers used strychnine as a means of trapping (Gunson 1983; Smith 1983).

The shrinking range of wolverines coincided with that of wolves in the late 1800's and the early 1900's. In some areas, predator control was coupled with the decimation of large mammal populations, such as the northern caribou herds (Heard 1983; Luttich 1983), reducing food available to wolverines. After the termination of widespread control in much of Canada, wolves recovered quickly but wolverines did not. This lack of recovery was most evident in eastern North America.

Wolverines and Wilderness

Wolverines appear not to tolerate land-use activities that permanently alter habitats, such as agriculture, and urban and industrial development. Unlike species such as coyotes (*Canis latrans*), black bears, raccoons (*Procyon lotor*), wolves, and some ungulate species in agricultural areas, wolverines generally do not eat the human foods that accompany human habitation. More than the actual loss of habitat or the

presence of humans, it is possible that the habitat fragmentation and access that result from land-use activities have the greatest impacts on wolverine.

CONSERVATION STATUS

A main theme that has emerged is that the information necessary for the management and conservation of wolverine populations in western forests is not available. Of paramount need is basic information on the occurrence and distribution of wolverines in the conterminous United States, and on whether these populations are self-sufficient or dependent on dispersers from Canada. With increaseing development and access in southwestern Canada and the northwestern United States, some populations may have already become isolated.

Until research can delineate the extent and nature of genetic variability among populations---and until research can determine whether wolverine ecotypes occur-then the conservative approach is to ensure that the range of variability is not degraded, either through loss of populations or continued population reductions. Although little information is available for mammals, higher genetic diversity at southern latitudes may characterize not only species but populations within species and genes within populations (Ledig 1993).

Because of the wolverine's large home range and extensive movements, it may appear that specific habitat attributes are not important and recolonization of vacant habitats is not a concern. However, natal and maternal dens may require a high degree of structural diversity and may be limiting in habitats that have been extensively modified by logging or other land-use practices. Insufficient denning habitat may serve to decrease the already low reproductive potential of wolverine. The dispersal of young females is likely the limiting factor in the recovery of vacant habitats. Successful recolonization may depend on sufficient recruitment from the source population and adequate dispersal corridors. Corridors that meet the needs of dispersing males may not do so for young females.

The key to maintaining wolverine populations is the establishment of large protected areas representative of the ecoregions that wolverine occupy and connected by adequate travel corridors. Refugia are important for providing dispersers to surrounding habitats, but it is unlikely that they will guarantee population persistence. Wolverine habitat needs must be accommodated at more than one scale: at the stand scale to meet requirements for food and dens, and at the landscape scale to meet requirements for home range sizes, travel corridors, and dispersal corridors.

The Future of Wolverine Populations

Wolverines in the western conterminous United States exist in small populations largely in inaccessible areas. Populations in northwest Montana have the greatest likelihood of long-term persistence because they are contiguous with protected areas in British Columbia and Alberta. The persistence of populations in Idaho, Oregon and northwest Wyoming are less certain but can be enhanced if connected large refugia are established within the Shining Mountains and the Northern Rocky Mountain Forest ecoprovinces. The Colorado population, if it still exists, may be isolated by the Wyoming and Central Rocky Mountain Basins. A recovery evaluation should consider whether the Colorado Rocky Mountains ecoprovince historically supported self-sustaining wolverine populations.

The future of wolverine populations in the Pacific Northwest Coast and Mountains ecoprovince is uncertain because of human settlement and dispersal barriers and possible isolation. Wolverines in the Sierra Nevada ecoprovince may already be isolated. Isolated populations maintained by refugia most certainly will survive in the short term. However, without dispersal corridors, their long-term persistence is in doubt.

With the current level of land-use activity, it may not be possible to provide sufficiently large refugia for wolverines where populations are not contiguous with habitat from British Columbia and Alberta. Even large national parks such as Yellowstone are considered too small to maintain self-sustaining populations of certain bears and other upper level carnivores (Soule 1980; Salwasser et al. 1987). An evaluation of whether there is sufficient habitat to support self-sustaining populations and to provide for dispersal corridors in the Pacific Northwest Coast and Mountains, Sierra Nevada, and Northern Rocky Mountain Forest ecoprovinces is required. Such evaluations will likely show that the long-term persistence of these populations is dependent on recovery efforts.

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ter of whom just recently was indoctrinated into the rigors of wolverine research.

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