

From: [Guinotte, John](#)
To: [Betty Grizzle](#)
Subject: Re: info needed on Idaho dens from the 90s.
Date: Tuesday, April 18, 2017 9:42:00 AM
Attachments: [Magoun and Copeland 1998 .img.pdf](#)

Sorry Betty, Here is the attachment.

John Guinotte
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On Tue, Apr 18, 2017 at 9:40 AM, Guinotte, John <john_guinotte@fws.gov> wrote:

Hi Betty,

I read through the Magoun and Copeland 1998 paper and need some information from them to do the temp analysis we spoke about yesterday.

See highlights in Table 1 of attachment. I need to know the lat/long and year for each of these natal dens so I can pull the daily temperature data for those locations. I also need some clarification on the statement *"In both Alaska and Idaho, abandonment of natal dens coincided with a period when maximum daily temperatures rose above freezing for a number of days for the first time since denning commenced."* I need to know how many days above freezing.

Thanks,
John

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Characteristics of Wolverine Reproductive Den Sites

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CHARACTERISTICS OF WOLVERINE REPRODUCTIVE DEN SITES

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Abstract: Successful wolverine (*Gulo gulo*) reproduction may be linked to the availability and quality of reproductive dens sites, but little is known about wolverine reproductive dens, especially in North America. We present descriptions of wolverine dens in Idaho and Alaska, compare them to dens in other regions, and propose factors that may influence den-site selection. Our study includes 8 den sites used by 3 females over 4 years in northwestern Alaska and 7 sites used by 2 females over 4 years in central Idaho. We categorized reproductive dens of wolverines as either natal (used during parturition) or maternal (used subsequent to the natal den and before weaning). Dens in Alaska were usually long, complex snow tunnels with no associated trees or boulders. In contrast, dens in Idaho were always associated with fallen trees or boulders. All dens were covered with at least 1 m of snow. With few exceptions, wolverine dens described to date have been located in alpine, subalpine, taiga, or tundra habitat. Reports of dens in low elevation, densely forested habitats are rare. Factors which may have influenced selection of den sites included thermoregulatory advantages, protection from predators, suitability of the site during the spring thaw, and location of rearing habitat. We recommend managers consider limiting wolverine harvests and reducing human disturbance in wolverine denning habitat.

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Key words: Alaska, conservation, den, *Gulo gulo*, habitat, Idaho, management, maternal, natal, reproduction, wolverine.

Information on habitat suitability is particularly lacking for the wolverine in comparison to other large carnivores in North America (Primm and Clark 1996). The wolverine occupies remote areas, is solitary and secretive, and occurs at relatively low densities, which makes field study difficult and expensive (Banci 1994). Locating wolverine dens is particularly difficult because researchers studying wolverines capture relatively low numbers of reproductive females. For example, in the 6 completed field studies of wolverines in North America, the combined sample of adult females was 34, of which only 7 were known to have produced kits (Hornocker and Hash 1981, Whitman and Ballard 1984, Magoun 1985, Banci 1987, Copeland 1996; D. A. Cooley, Yukon Department of Renewable Resources, unpublished data).

Detailed descriptions of reproductive dens have come primarily from Fennoscandia, provided by hunters who snow-tracked females to dens and then excavated kits (Myrberget 1968, Pulliainen 1968). Length of time that dens were occupied and past use of denning sites were largely unknown in the above studies. Because detailed descriptions of reproductive dens in

North America do not exist, we present information on dens of marked females radiotracked in successive years in Idaho and Alaska. We also review the literature on characteristics of wolverine dens from other regions and propose factors that may influence den-site selection. Finally, we discuss how characterizing wolverine denning habitat might influence wolverine conservation and management.

STUDY AREA AND METHODS

As part of broader studies on wolverine ecology (Magoun 1985, Copeland 1996), we collected data on reproductive dens of wolverines from 1978 to 1981 in northwestern Alaska (Magoun), and from 1993 to 1996 in central Idaho (Copeland). The Alaska study area (69°N, 161°W) was treeless tussock tundra and alpine ridges in the northern foothills of the western Brooks Range, with elevations of 300–1,250 m. The Idaho study area (44°N, 115°W) was mountainous habitat in the Sawtooth, Challis, and Boise national forests, with elevations of 1,400–3,279 m characterized by densely forested lower mountain slopes and valley bottoms, midslope forests interspersed with savanna grasslands, and higher elevation subalpine forests associated with talus and cirque basins. Treeless alpine habitat occurred above 2,700 m.

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Despite low snowfall in the Alaska study area, frequent high winds created dense, hard-packed snowdrifts often >4 m deep along drainages and gullies. Snowfall measured at a weather station in Umiat (370 km east of the study area in similar tundra habitat) never exceeded 0.5 m during the study period. In Idaho, deep snow (0.5–2.5 m) was uniformly distributed on the forested mountain slopes and was not generally dense and hard packed, except in exposed alpine areas. The average monthly temperature (°C) in the Idaho study area for the 4 years of the study ranged from –8 to –2 in February, –4 to –1 in March, and –1 to +2 in April. Temperatures measured at Umiat during the 4 years of the Alaska study were –32 to –25 in February, –30 to –24 in March, and –20 to –16 in April. Temperatures in the Alaska study area generally did not rise above freezing until late April or early May, whereas temperatures in Idaho commonly rose above freezing during the entire denning season.

We refer to February–April as the denning season. We categorized wolverine reproductive dens as either natal (used during parturition) or maternal (used subsequent to the natal den and before weaning). Dens used after weaning were considered rendezvous sites (Magoun 1985, Copeland 1996) and are not addressed in this paper. We used 10 weeks after parturition as the weaning date and estimated date of parturition by comparing tooth eruption, body size, or pelage coloration of the kits to that of known-age, captive wolverine kits (C. Long, Carcajou Research Centre, unpublished data; D. N. Pedersen, United Farms, unpublished data).

We located reproductive dens of wolverines primarily by radiotracking >22-month-old female wolverines from aircraft. Repeated locations of a female at the same site during the denning season identified a possible den site. Radiotracking >20 times during the denning period established the time frame in which the site was used. If the female was later seen with kits or if tracks of kits were seen at the site, the den was confirmed as a reproductive den. If we could not verify that kits were produced, we considered the den a reproductive den if the female was known to have produced kits in the past and her radio signal was received >10 times from the den for >1 week during the denning season (see DISCUSSION). We discovered 1 den site in Alaska by radiotracking an adult male during April to a snow tunnel that

had numerous tracks of kits radiating from the entrance, and we located another den site by radiotracking a female to a den in late March and excavating kits from the den in early April.

We usually excavated dens when radio locations of adult females indicated they were no longer using the dens. Excavation of a den in Alaska while kits were present was necessary because the radio of the adult female was failing. A portion of the den was not excavated in order to leave some protection for the kits until the female returned to the den. As dens were excavated, we took measurements on length, width, and depth of snow tunnels, and we recorded other features. Because some melting had occurred before dens were excavated, complete excavations were not usually possible. In Idaho, fewer dens were excavated because tunnels and chambers within boulder talus were inaccessible.

We established timing of the spring thaw in Alaska through direct observation while living in the study area during the denning period, and from temperature records taken at Umiat. To estimate spring thaw for the Idaho study area, we examined records of snow water equivalent (SWE) taken at the Banner Summit SNOTEL Station during February, March, and April. This station was in the home range of 1 of the denning females. The SWE is based on the mass of the snow. A drop in SWE occurs when the snowpack warms, becomes saturated with water, and runoff begins. The SWE measurements were not available for the Alaska study area.

RESULTS

In Alaska, we collected data at 8 sites used by 3 females (Table 1). At 4 sites, we verified presence of kits but did not establish the date when the female began denning. In 2 other cases, we documented the date denning was initiated. However, these 2 dens were abandoned 8–12 days later, and the females did not raise kits that summer. We believe parturition occurred at all 6 dens for reasons given in the Discussion, and we refer to these dens as natal dens. The remaining 2 sites were verified as maternal dens.

In Idaho, we collected data from 7 sites used by 2 females (Table 1). Two sites were verified natal dens and 5 were maternal dens. One of the natal dens was used by the same female in 3 consecutive years. In 1994, this den had 3

Table 1. Reproductive dens of wolverines in Alaska (AK) from 1978 to 1981, and Idaho (ID) from 1993 to 1996.

Natal den	Associated maternal den	Female	Den first located	Den abandoned	Estimated parturition date	No. of kits	Possible days occupied
AK1-78 ^a		Unmarked	28 Apr	Unknown ^b	Unknown	Unknown	Unknown
AK2-79 ^a		F7	19 Mar	29 Apr	24 Feb	2	42-65
	MD1 _{AK2}		5 May	9 May			5-11
AK3-80 ^c		F7	7 Mar	15 Mar	Unknown	Unknown	9
AK4-81 ^a		F7	4 Apr	Unknown ^b	4 Mar	2	Unknown
AK5-79 ^a		F10	16 Mar	18 Apr-5 May	6 Mar	2	34-61
	MD1 _{AK5}		5 May	9 May ^b			5-22
AK6-80 ^c		F10	4 Mar	15 Mar	1 Mar	Unknown	12-15
ID1-93		F502	14 Feb	4-10 Mar	18 Feb	2	19-25
	MD1 _{ID1}		10 Mar	29 Mar-4 Apr			20-26
	MD2 _{ID1}		5 Apr	14 Apr ^b			10-17
	MD3 _{ID1}		26 Apr	30 Apr ^b			5-17
ID2-94		F703	20 Feb	7-14 Mar	23 Feb	2	16-23
	MD1 _{ID2}		14 Mar	26 Mar-7 Apr			13-25
	MD2 _{ID2}		8 Apr	24 Apr ^b			17-30
ID3-95		F703	16 Feb	29 Mar-4 Apr	16 Feb	2	42-48
	MD1 _{ID3}		3 Apr	17-20 Apr			15-18
ID4-96		F703	29 Feb	Unknown	Unknown	Unknown	Unknown

^a Date of den initiation unknown.^b Disturbance by researchers at the den may have caused premature abandonment.^c Wolverine kits not seen with the female after den abandonment.

maternal den sites associated with it. In 1995, the female used 1 of the maternal den sites from the previous year. Data were not collected on maternal den sites in 1996.

Natal Dens

The 6 natal dens in Alaska were in deep snowdrifts along minor drainages at elevations of 560-625 m. We excavated 5 of the 6 dens, but only 2 in their entirety. The 5 excavated dens were complex, extensive systems of snow tunnels averaging >30 m in length. All 6 dens had only 1 entrance. One den had another snow tunnel entrance near it, but this tunnel did not connect with the den, did not appear well used, and was not excavated. Tunnel entrances were 25-35-cm-wide holes in snow from which tunnels dropped steeply for about 1 m at an angle slightly less than vertical. From this point, tunnels were more or less horizontal and rarely reached ground level. Depth of tunnels from the surface of the snowdrift usually increased as the tunnels extended deeper into the drift. Width of tunnels was usually 30 cm, except where tunnels widened into beds that were 40-90 cm wide. Total tunnel length ranged from 14 to 54 m ($n = 5$), but the dens with the shortest and longest tunnel systems were not excavated in their entirety. The number of side tunnels ranged from 0 to 10 and averaged 5/den, although not all tunnels were excavated. The di-

rection of tunnels often changed when tunnels reached dense shrubs or tussocks, although structures were not always present when tunnels changed direction. Some tunnels had no structures associated with them. Depth from the snow surface to the deepest point in the tunnel systems was >1 m; the maximum depth measured was 2.4 m.

In natal dens in Alaska, number of beds ranged from 1 to 8 and averaged 5, although some beds may have melted before excavation and were not recorded. There did not appear to be any special preparation of the beds other than an enlargement of the snow tunnel. Heavily used beds were icy and hard packed. Most beds were within the snow layer and had no vegetation or other insulative material. However, 2 of 30 beds were on broken branches of shrubs at ground level. The 2 kits dug from a den were huddled on bare, icy snow in a bed 1.5 m deep and about 18.5 m from the tunnel entrance.

The 2 natal den sites in Idaho were snow tunnels that accessed snow-covered boulder talus in subalpine cirque basins located above 2,500 m. The dens were in open areas <100 m wide and surrounded by trees on generally north-facing slopes. A number of chambers and branching passageways were naturally formed within the boulder talus. The first natal den site had only 1 entrance and consisted of a snow tunnel

about 2 m long that descended at a 40° angle into the talus. Further excavation of the den was not possible. The second natal den site, used by another female in 3 consecutive years, was only excavated in the first year. Three entrances were present at that time: 2 under large adjoining boulders, and 1 under boulder talus about 23 m from the first 2 entrances. We saw 3 entrances from the air in 1995, but only 1 in 1996. Well-used beds were not evident in excavated portions of the dens.

Maternal Dens

Of the 2 known maternal dens in Alaska, 1 was under a remnant snowdrift where meltwater had created a tunnel, and 1 was in a rock cave. They were 3.8 and 3.2 km from their respective natal dens and at about the same elevation as the natal dens. In Idaho, the maternal dens were usually a complex of either separate "dens" 100–400 m apart, or more proximate "dens" with several adjacent entrances 5–40 m apart, some of which may have been interconnected. The dens were usually snow tunnels leading to naturally formed chambers beneath either large boulders (9 tunnels from 6 sites) or fallen trees (6 tunnels from 4 sites). One tunnel descended downward beside a standing spruce (*Picea engelmannii*) tree but was not excavated. The longest tunnel excavated was >22 m. The distances between 3 natal dens and the first subsequently used maternal dens were 0.7, 1.0, and 2.6 km. The distances between 3 consecutively used maternal den sites were 1.5, 2.4, and 2.9 km. Females used 1–3 maternal dens/year. All but 1 of the maternal dens in Idaho were located at somewhat lower elevations than the natal dens, with the greatest drop in elevation being about 300 m.

Den Abandonment

In both Alaska and Idaho, abandonment of natal dens coincided with a period when maximum daily temperatures rose above freezing for a number of days for the first time since denning commenced. The spring thaw in Alaska occurred rapidly in 1979, arriving 2 weeks earlier than in 1978, 1980, or 1981. The maximum daily temperature recorded at Umiat rose above freezing for the first time on 20 April 1979 and exceeded the freezing point every day thereafter. Den abandonment that year occurred on 29 April for 1 denning female and between 18 April and 5 May for the other female. The mea-

sured snowpack at Umiat dropped from 0.5 to <0.1 m from 20 April to 29 April. When we excavated the dens of the 2 females on 7–8 May, we encountered standing water and slumping tunnels at 1 site. At the other, whole sections of the tunnel system had melted away. In contrast, a reproductive den used by an unmarked female in 1978 was still intact and appeared recently occupied when it was excavated on 6 May. The maximum daily temperature in Umiat in 1978 rose above freezing only on 14–15 April and did not go above freezing again until 1 May.

The timing of natal den abandonment in Idaho was earlier than in Alaska and varied by as much as 1 month (Table 1). Natal den abandonment in Idaho occurred during 4–10 March in 1993, 7–14 March in 1994, and 29 March–4 April in 1995. In all 3 years, abandonment of natal dens corresponded to a period when SWE at Banner Summit dropped by 0.25–1.00 cm for the first time since denning commenced. Moves between maternal den sites that were not influenced by human disturbance occurred during subsequent drops in SWE.

Kits in the Idaho study area were an estimated 13–20 days old when first moved from the natal den in 1994, but 42–48 days old in 1995 (Table 1). In Alaska, kits may have been >60 days old when they were moved from their suspected natal dens in 1979, a year with an unusually early spring thaw.

We often visited 1 of the natal dens in Alaska on snowmachines and snowshoes during the denning period, but the female did not abandon the den until the spring thaw. Although she was livetrapped near her den to replace her collar on 21 April, this female did not abandon the den until 29 April. However, when females in the Alaska study area began using maternal dens and rendezvous sites, they moved their kits within hours of detecting researchers in the area.

In Idaho, we did not visit natal den sites during the time the dens were occupied, except to fly overhead while radiotracking, but we did visit some maternal den sites. One female moved her kits 330 m from 1 maternal den to another on the day following our visit. She moved 2.9 km to a new maternal den complex soon after we excavated the original site. She moved again 16 days later when we visited the new maternal den complex. The other female moved her kits from a maternal den within 1 hr of discovering

our presence nearby. These moves occurred between 13 and 26 April.

DISCUSSION

Descriptions of wolverine dens from the literature do not provide enough details to determine if the dens referred to were natal dens, maternal dens, or rendezvous sites. In the Fennoscandian studies, which provided data on the largest number of reproductive dens from any region ($n = 59$), the proportion of dens that were natal dens cannot be determined (Myrberget 1968, Pulliainen 1968). In a study of American marten (*Martes americana*), Ruggiero et al. (1998) emphasized the importance of using precise terminology and explicitly discriminating between sites used for parturition (natal dens), sites where kits were present exclusive of parturition (maternal dens), and resting sites not associated with reproduction. In their study, natal and maternal dens were critical to marten recruitment, and marten appeared most selective in choosing natal den sites.

Verifying that a site is a wolverine natal den is difficult because initiation of denning and the presence of kits must be established. Obtaining this information is time consuming and expensive and usually requires frequent tracking of females in remote areas prior to, during, and after the denning season. Data from the study area in Idaho show that moves from a natal den can occur when kits are as young as 13 days old, and females may move kits ≥ 3 times before they are weaned. We did not locate 4 dens in the Alaska study area until at least 10 days after the kits were born, which made it impossible to verify they were natal dens. However, we believe these 4 dens were natal dens because spring thaw did not occur in the Alaska study area until late April or early May, and we did not document moves between reproductive dens in either study area before thaw conditions occurred, except when we disturbed the den sites.

We believe that dens used by 2 parous females in Alaska in 1980 were natal dens, although kits were not raised by the females that summer. Both of these females raised 2 kits in 1979, and at least 1 of the females raised 1 kit in 1978 and 2 kits in 1981. Both females were located in the dens >10 times over a period of 8–12 days in early March. Of 42 wolverines radiomarked in our study areas (Magoun 1985, Copeland 1996), only females with kits and the

2 parous females in 1980 demonstrated such fidelity to a particular site, and only during the denning season. There was no evidence of food at the 2 sites in 1980 that could account for the fidelity of the females to the sites.

Den Location and Structure

Characteristic areas where wolverines den include ravines or drainages where snow accumulates (Pulliainen 1968, Serebryakov 1984, this study), snow-covered rocky scree or boulder talus (Haglund 1966, Myrberget 1968, Pulliainen 1968, Lee and Niptanatiak 1996, this study), snow-covered fallen trees usually near timberline (Pulliainen 1968, Zyryanov 1989, this study), taiga peat bogs with rocky areas or fallen trees (Pulliainen 1968), and birch (*Betula* spp.) woodland near fells or alpine areas (Pulliainen 1968, Landa et al. 1998a). Particular sites may be used repeatedly for denning (Pulliainen 1968, Lee and Niptanatiak 1996, this study). Almost all verified wolverine reproductive dens were under 1–5 m of snow. Most consisted of relatively long, complex snow tunnels, often associated with fallen trees or large rocks, or shorter snow tunnels leading to inaccessible boulder scree. Less typical dens include 1 at the base of a spruce (*Picea* spp.) tree in January (Pulliainen 1968), and 1 in an abandoned beaver (*Castor canadensis*) lodge (Rausch and Pearson 1972).

With few exceptions, wolverine reproductive dens have been located in alpine, subalpine, taiga, or tundra habitat (Haglund 1966, Myrberget 1968, Pulliainen 1968, Bjärvall 1982, Serebryakov 1984, Zyryanov 1989, Lee and Niptanatiak 1996, Landa et al. 1998a, this study). Rarely have dens been reported in low-elevation, densely forested habitats, although wolverines occupy these habitats. Two of 25 reproductive dens in Norway were found in mixed pine (*Pinus* spp.) and birch forest at 200 m elevation, but no details on the structure or dates of the 2 dens were presented (Myrberget 1968). We were able to verify only 1 report of wolverines denning in lowland forested habitat in North America, the abandoned beaver (*Castor canadensis*) lodge reported by Rausch and Pearson (1972).

Banci (1994) speculated that most reproductive dens reported in tundra habitat may be an artifact of where researchers have searched for dens, and she recommended more effort to locate dens in forested habitat. However, the 2

females in the Idaho study area had home ranges that included continuous, densely forested habitat at lower elevations, but they denned in more open areas at higher elevations. Moreover, Bjärvall (1982) located 4 reproductive dens above treeline, although 52% of the area used by the denning females was coniferous forest. The females obtained nearly all their food in the forest during the denning period, carrying food back to the alpine dens from as far away as 22 km.

We believe a critical feature of wolverine denning habitat is dependability of deep snow throughout the denning period. At least 1 m of snow, distributed uniformly or accumulated in drifted areas, should be present by February and persist until May. Location of wolverine reproductive dens under deep snow confers a thermoregulatory advantage to kits, which are born when winter temperatures still prevail (Pulliainen 1968, Bjärvall et al. 1978). Boulder talus and fallen trees are incorporated into reproductive dens if they are available and covered with deep snow. Snow-covered boulders and fallen trees provide natural subnivean cavities and may attract wolverines because they are visually obvious. Dens which did not incorporate boulders or fallen trees were found at higher elevations or latitudes in drifted, hard-packed snow (Pulliainen 1968, this study).

Protection From Predators

A number of large mammalian predators, as well as golden eagles (*Aquila chrysaetos*), are suspected or known to kill wolverines (Hornocker and Hash 1981, Banci 1994, Copeland 1996), and kits may be particularly vulnerable to predation when kept at insecure sites or moved between sites. Five gray wolves (*Canis lupus*) were observed killing wolverine kits on 20 March 1983 in forested habitat along the Chilkat River in Alaska (K. J. Hundertmark, Alaska Department of Fish and Game, personal communication). The amount of snow the wolves had excavated was minimal, which indicates the kits had not been dug from a deep snow tunnel. Long, complex snow tunnels protect kits from predators because of the effort required to dig kits from deep snow (Pulliainen 1968, this study). Reproductive dens that incorporated fallen trees also had long snow tunnel systems (Pulliainen 1968, Zyryanov 1989, this study). Dens in boulder talus are probably among the most secure sites for reproductive

dens. Wolverines in Idaho used dens associated with boulder talus early in the denning period and only later moved their kits to dens associated with fallen trees.

Besides constructing dens that protect kits from predation, wolverines may den in areas with low populations of potential predators relative to other areas and other times of the year. Krott (1982) stated that wolverines avoid wolves by retreating into mountainous regions, large bogs, or areas with long-lasting, deep snow cover. In our study, large mammalian predators were absent from denning areas until late April or May (Magoun 1985, Copeland 1996).

Myrberget (1968) stated that a female wolverine will often leave her den with her young if she feels threatened. In the Alaska study area, adult females did not move their kits from natal dens when humans were in the area unless the dens were disturbed, but females quickly moved their kits from maternal dens and rendezvous sites when they detected researchers in the general vicinity of dens. Maternal dens may not be as secure from predators as natal dens, and reproductive females may be more sensitive to low-level human disturbance at maternal dens than at natal dens.

Proximity to Rearing Habitat

Reproductive females may be influenced in their selection of denning habitat by its suitability as rearing habitat for kits after weaning. Researchers have documented seasonal shifts by some wolverines from lower elevations in winter to higher elevations in summer (Hornocker and Hash 1981, Whitman et al. 1986, Banci 1987, Copeland 1996), and Whitman et al. (1986) postulated that shifts to higher elevations in summer were in response to food availability, primarily small mammals and birds. Wolverines are usually characterized as scavengers or opportunistic omnivores (Banci 1994), but their role as a predator of small mammals and birds may be more important to the rearing of kits than is their role as a scavenger (Myrberget and Sørungård 1979, Magoun 1987, Copeland 1996, Landa et al. 1997).

Bevanger (1992) stated that opportunities for hunting are severely reduced for the wolverine in summer, and that storing and conserving food in swamps, rocky scree, and snowdrifts is an advantage to wolverines. During summer in our study areas, wolverines made food caches beneath remnant snowdrifts, in cold tundra cov-

ered with vegetation, and in cool areas under talus. High elevation and high latitude habitats probably provide more options for food storage in summer than do low-elevation forests.

MANAGEMENT IMPLICATIONS

Characterizing suitable wolverine denning habitat has a number of conservation and management implications. Krott (1959) believed the availability of denning habitat may influence the size of wolverine territories, and Landa et al. (1998b) proposed a population estimator for wolverine based on the number of active reproductive dens. Wolverine productivity and population maintenance may be linked to availability and quality of reproductive den sites (Banci 1994). However, more research is needed on identifying wolverine denning areas, developing den surveys to establish the number of reproductive females and denning activity, and understanding the effect of human activities on denning wolverines.

The perpetuation of wolverine populations in the conterminous United States, where wolverine habitat is limited and discontinuous, may depend upon resolving conflicts between human activity and the protection of wolverines in remote mountainous landscapes (Banci 1994, Copeland 1996). Protection should extend not only to denning and foraging habitat but also to travel and dispersal corridors between these habitats (Banci 1994, Landa 1997).

In Alaska, where wolverines essentially occur statewide, concern for effects of human activities on wolverine denning and reproduction is greatest near large human populations. Over broader areas of Alaska, management concerns focus on regulation of wolverine harvests. Presently, harvest quotas and seasons are based on historical harvests, not on known recruitment or estimates of harvestable surplus, although there are ongoing efforts to develop density estimators (Golden 1997, Becker et al. 1998).

McCullough (1996) argued that a species regulated under a system lacking population data is vulnerable to overharvest, and maximum sustained yield is not achievable. He recommended a system of spatial controls through a mosaic of hunted and unhunted areas, which will be resistant to unintended overharvest and has the advantage of lacking a requirement for population data. We believe a spatial control system of harvest regulation for wolverines should be centered on regions of wolverine reproduction

and would require managers to identify wolverine denning areas that are sources of dispersers to trapped areas (Dias 1996). When limits to harvest are necessary, harvests of wolverines could be curtailed in blocks identified as prime denning habitat distributed across landscapes in which denning occurs. The size of protected areas would depend upon factors such as proximity and extent of suitable habitat and areas already closed to trapping, size of reproductive female home ranges, seasonal availability of food and its effect on movements, and human access and activities.

A system of refugia for managing wolverines has been proposed by a number of authors (Hatler 1989, Banci 1994, Weaver et al. 1996). The refugia concept is similar to the spatial harvest control system proposed by McCullough (1996). Hatler (1989) recommended that trappers in British Columbia who wish to ensure a long-term, consistent supply of wolverines maintain refuges or untrapped areas on their traplines in more inaccessible areas near or above timberline.

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