

From: [Inman, Bob](#)
To: [Grizzle, Betty](#)
Subject: RE: GYE wolverine dens
Date: Tuesday, May 30, 2017 4:18:18 PM
Attachments: [4 Reproductive Rates and Maternal Habitat REPORT.pdf](#)

Hello Betty, page 5 has some info in results. This is from a 2007 report from our study that had 8 chapters, 4 of which are published now. This was a general proximity measurement. I can remember going to a den in the Gravelly Mtns, sticking my ski pole in the snow to stand it up there while beginning to record data about the den, and when I stuck the pole into the snow, to my surprise it went 6" or so through the snow and then through a few sticks, and when I looked down a wolverine was looking back up at me through the hole. So there was as little as 6" of snow over parts of a natal den. While standing there, we did not know where all the den actually was below the snow and debris, so we just took a general measurement in the vicinity. Those are what is in the attached. This was occurring before any discussion about "deep" or "persistent" spring snow, so we were not thinking to make lots of exact measurements all around the site. Also wanted to get in, more the locaitons, and get out, in case our presence was disturbing in some way.

As an anecdote,

-Bob Inman

Robert M. Inman, PhD
Carnivore-Furbearer Coordinator
Montana Fish, Wildlife and Parks
1420 East 6th Ave., PO Box 200701,
Helena, MT 59620-0701
406-444-0042 (o)
406-570-5326 (c)
bobinman@mt.gov

From: Grizzle, Betty [mailto:betty_grizzle@fws.gov]
Sent: Wednesday, May 24, 2017 10:33 AM
To: Inman, Bob <bobinman@mt.gov>
Subject: GYE wolverine dens

Hi Bob - Did you measure snow "depth" or "cover" for your GYE wolverine den locations (at or near the time of denning)? If so, can you send me those values and the dates measured?
Thanks, and please let me know if you have questions.

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Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service

Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

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Wolverine Reproductive Rates and Maternal Habitat in Greater Yellowstone

ROBERT M. INMAN, *Wildlife Conservation Society, 2023 Stadium Drive 1A, Bozeman, MT 59715, USA, and Swedish University of Agricultural Sciences, Dept. of Ecology, Grimsö, SE - 730 91 Riddarhyttan, Sweden*

KRISTINE H. INMAN, *Wildlife Conservation Society, 2023 Stadium Drive 1A, Bozeman, MT 59715, USA*

MARK L. PACKILA, *Wildlife Conservation Society, 2023 Stadium Drive 1A, Bozeman, MT 59715, USA*

ANTHONY J. MCCUE, *Wildlife Conservation Society, 2023 Stadium Drive 1A, Bozeman, MT 59715, USA*

ABSTRACT Documentation of wolverine (*Gulo gulo*) reproductive rates and maternal habitat is crucial for developing conservation strategies for the species in the conterminous U.S. Prior to initiation of this study, reproductive data from the conterminous U.S. was limited to observations of 13 female-years, 4 litters, and 2 natal dens. We studied wolverines in the Greater Yellowstone Area (GYA) of Idaho, Montana, and Wyoming where we captured 17 female wolverines between January 2002–May 2007 and monitored them for reproduction during 40 female-years. Based on observations of known-age females and estimates of minimum possible age at first capture, reproduction at <4 years appears to be uncommon, and at least 1 female had not given birth by 5 years of age. Proportion of adult (≥ 3 years of age) females reproducing was 0.26 ($n = 23$ adult-female-years) and annual birth rate was 0.30 cubs/adult female/year ($n = 23$ adult-female-years). Mean litter size was 1.1 cubs ($n = 7$ litters). We estimated a minimum interbirth interval of 2.3 years ($n = 7$) based on several assumptions that could only bias the estimate low. Recruitment rate was 0.27 cubs/adult female/year ($n = 15$ adult-female-years). Mean parturition date was 16 February. Elevation of natal dens ($n = 5$ specific sites and 2 general sites) ranged from approximately 2,200–2,822 m (7,218–9,259 ft). The primary structural component of the 5 specifically identified natal dens was avalanche debris consisting of downed logs, and macro aspect was north at each of these sites. Six of 7 natal dens were located in designated wilderness (4), a wilderness study area (1), or a National Park (1); one natal den was located in a multiple use area that was occasionally used by snowmobilers. Natal dens were typically used through at least late April and use of maternal dens was rare. Rendezvous sites ($n = 9$) were located at a 2,195–2,865 m elevation (7,201–9,400 ft) and ranged from 2.3–14.7 km from their respective natal dens. The primary structure at rendezvous sites was large boulders (44%), logs in avalanche debris (33%), or downed logs (22%); snow >1m was common at these sites during May and June. Eighty-one percent of natal dens and rendezvous sites ($n = 16$) were located in subalpine habitats, near timberline, where boulder talus and open meadows were interspersed with forested areas. Two natal dens and one associated rendezvous site occurred at lower elevation in heavily forested areas. Reproductive rates of wolverines in GYA appear to be as low as or lower than rates reported from other areas. Given the inherently vulnerable nature of wolverine populations in general and the possibility that this vulnerability could be exacerbated in the conterminous U.S. because of the island-like nature of habitat, conservation strategies for wolverines therein should include efforts to limit mortality of adult females and insure that reproductive capacity is not compromised in any way. While successful reproduction is likely critical in all habitats used by a metapopulation of wolverines in the conterminous U.S., reproduction in smaller mountain ranges that are in-between “regional population centers” (RPCs) may be of greatest importance given their increased likelihood of accomplishing genetic exchange among RPCs.

KEY WORDS den, *Gulo gulo*, habitat, reproduction, wolverine, Yellowstone.

Wolverines are inherently vulnerable because they exist at low densities and reproduce slowly (Banci 1994, Persson et al. 2006, Inman et al. 2007a). The conterminous U.S. represents the southern extent of the wolverine’s global distribution (Copeland and Whitman 2003), and primary habitat in the Rocky Mountain states exists in rather island-like fashion (Brock et al. 2007). Populations there are influenced by numerous political jurisdictions (Inman et al. 2007a), and areas of historic distribution (e.g., Colorado) do not appear to be occupied at present (Aubrey et al. 2007). Therefore vulnerability of the species is likely exacerbated in this region.

Wolverines may also be sensitive to human activity (Copeland 1996, Magoun and Copeland 1998), and managers suggest that numbers of backcountry recreationists during winter are increasing on public lands (Greater Yellowstone Coordinating Committee 1999). Advances in snowmobile engineering along with use of helicopters to access extreme ski terrain have made it possible for recreationists to access areas that have historically been refugia for wolverines. Energetics

does affect reproductive capacity of wolverines (Persson 2005), thus maternal habitat (natal dens, maternal dens, and rendezvous sites; Magoun and Copeland 1998) is a prime concern because lactation and post-weaning growth are the periods of most intense energetic demand (Ofstedal and Gittleman 1989, Inman et al. 2007b). In addition, juvenile survival could be lowered if additional moves among den sites occurs due to human activity (Magoun and Copeland 1998). Wolverines are harvested in Montana, and given the potential for significant population influences via human-induced mortality (Krebs et al. 2004, Squires et al. 2006, Inman et al. 2007c), determining appropriate levels of harvest depends on adequate reproductive data.

Development of strategies for maintaining reproductive capacity of wolverine populations is crucial for persistence. However, data on wolverine reproductive rates and denning habitat are sparse and the vast majority were obtained in areas where caribou (*Rangifer tarandus*) are abundant and other ecological factors differ greatly from the conterminous U.S. (Pulliainen 1968, Rausch and Pearson 1972, Magoun 1985,

Persson et al. 2006). Prior to initiation of this study, data on wolverine reproduction in the conterminous U.S. was limited to monitoring 6 females over 13 female-years and documenting habitat characteristics at 2 natal and 6 maternal den sites in central Idaho (Copeland 1996, Magoun and Copeland 1998). Clearly additional information on wolverine reproductive rates and denning habitat in the conterminous U.S. is needed for developing conservation strategies in this region. Our goal was to document reproductive rates, timing of reproductive events, characteristics of maternal habitat, and maternal food habits of wolverines in the Greater Yellowstone Area (GYA).

STUDY AREA

Our research occurred on two focal areas (Madison and Teton, Fig. 1) within GYA, a 108,000 km² ecosystem geographically based on the Yellowstone Plateau and 14 surrounding mountain ranges in Idaho, Montana, and Wyoming (Marston and Anderson 1991, Patten 1991, Noss et al. 2002). Elevations ranged from approximately 1,400 to 4,200 m. Precipitation increased with elevation and varied from 32–126 cm (NRCS 2007). Snow usually fell as dry powder and depths at higher elevations were often in excess of 3.5 m. The diverse physical aspects of the study area result in a variety of vegetative communities (Despain 1990). Low elevation valleys often have short grass prairie or sagebrush communities. The transition to forest often occurs with Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*). Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) become more common as elevation increases. The highest elevations were alpine tundra or talus fields and snow was typically present for at least 9 months of the year (NRCS 2007). A diverse fauna was present (Bailey 1930, Streubel 1989) and included a variety of ungulates and carnivores that are not found in many areas where wolverines exist.

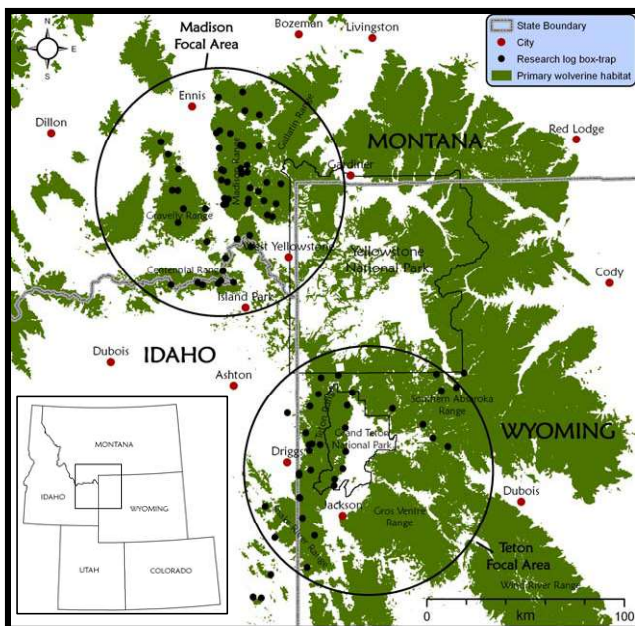


Figure 1. Madison and Teton study sites of the Greater Yellowstone Wolverine Program, Montana, Idaho, and Wyoming, USA, 2000–2007.

METHODS

Capture, Monitoring, and Age-classification

We captured wolverines during winters of 2000–2007 in log box traps (e.g., Copeland et al. 1995, Krebs and Lewis 2000) equipped with trap-transmitters (Telonics, TBT-500, Mesa, AZ, USA). We also captured juvenile wolverines by hand at den or rendezvous sites (Persson et al. 2006). We used a variable-powered CO₂ pistol (CO₂ PI, Dan-Inject, Fort Collins, CO, USA), a syringe pole, or a hand syringe to deliver an initial dose of 8.0mg/kg ketamine + 0.05mg/kg medetomidine + 0.40mg/kg turbogezic (Quigley 2000) or approximately 7.5mg/kg ketamine + 0.25mg/kg medetomidine (Arnemo 2006, Atkinson 2006). We surgically implanted all wolverines with an intra-peritoneal VHF radio-transmitter (Telonics Imp400L, Imp300L, Mesa, AZ, USA; Advanced Telemetry Systems M1250, M1245, Isanti, MN, USA). We followed handling procedures approved by the Animal Care and Use Committees of the Hornocker Wildlife Institute/Wildlife Conservation Society (2000-RMW-504, 2000–2006) and Montana Department of Fish, Wildlife and Parks (IACUC 1–2006, 2006–2007) as permitted by U.S. Department of Agriculture, Animal and Plant Health Inspection Service (Permits 81-R-0015 and 81-R-0018). We attempted to collect aerial VHF telemetry locations at an approximate 10 day interval. We also fit 11 wolverines with global positioning system (GPS) collars programmed to collect locations at various intervals (Televilt POSREC 300, Telemetry Solutions, Concord, CA, USA; Lotek Wireless Inc. 3300SL, Newmarket, ON, Canada). (Note: 5 additional females were fit with GPS collars during January and February of 2007, but those data are not all available at present). We assigned ages based on a known age (cub captures at dens) or cementum annuli. While age estimates via cementum annuli for wolverines are imprecise (J. Persson, Swedish University of Agricultural Sciences, unpublished data), no technique other than cub captures at dens is available. Based on reproductive maturity of female wolverines (Persson et al. 2006) and the age through which dispersal movements continued (Inman et al. 2007a), we classified wolverines ≥3 yrs old as adults and <3 yrs as subadults. Subadults referred to as juveniles or cubs were <1 yr old, and those referred to as yearlings were between 1–2 years old.

Reproductive Parameters

Proportion of females reproducing each year.—We attempted to aerially locate each female at least two times per week during the den initiation season (15 January–15 March) to find clusters of locations or other indications of active den sites (Magoun and Copeland 1998, Persson et al. 2006). At the first instance of a female being located at the same spot >3 times during the reproductive season, we visited the site to flag the location and initiated efforts to confirm a reproductive event at the appropriate time (i.e., capture or observe cubs). When a female was not located repeatedly at the same site, we classified that female-year as a non-reproductive event. Weather often limited the number of telemetry flights we were able to conduct, thus it is possible that births may have occurred without our detecting a concentration of locations at a den. However, although females may remain exclusively at the natal den site

for as few as 4 days, they return frequently to the den site and remain there for extended periods (J. Persson, unpublished data). Therefore it is unlikely that we did not detect a concentration of locations unless the litter was lost within a few weeks of birth. We also attempted in many cases to observe females during May–June to make sure that we did not miss production of a litter. We calculated the proportion of females ≥ 3 years of age reproducing each year based on confirmed reproductive events or lack of denning behavior and no observation of cubs.

Litter size and annual birth rate.—Capture of cubs at a den could result in underestimation of litter size because of the intricate structure typically existing at a den, i.e. deep snow covering a tangled mass of logs and limbs in an avalanche debris pile that can contain tens or possibly hundreds of small chambers (see photos below). Cubs are capable of moving among the crevices within the debris, and often an absolutely complete search is not possible. Cub tracks in the snow while traveling with the female provide more satisfactory evidence of cub numbers, but could underestimate litter size if cubs are moved one at a time or stashed in different locations. If denning occurred or a cub was detected, we made several attempts to observe the family group in order to increase the certainty of how many cubs were present. We calculated annual birth rate as the average of the number of cubs known to be born divided by the number of adult (≥ 3 yr) females being monitored each year (Persson et al. 2006).

Age at first reproduction.—We determined production of a litter by known-age females as described above. We also used information on date of first capture for all females that had not given birth prior to our first capture (i.e., teat condition indicated they were nulliparous) to estimate a minimum age at which each female had either reproduced or not. We did this by assigning an age of zero years (captured at 10–12 months of age) to each nulliparous female at her first capture.

Interbirth interval and recruitment rate.—We calculated interbirth interval as the mean number of years between documented litters. We also provide an additional estimate of a minimum interbirth interval with assumptions based on *in utero* examinations, teat condition at first capture, and reproduction during the upcoming (2008) den season. We calculated recruitment rates as the number of cubs per adult-female-year known to be alive on 1 March of the year following birth (Persson et al. 2006).

Timing of Reproductive Events, Maternal Habitat, and Maternal Food Habits

Parturition date and timing of natal den, maternal den, and rendezvous site use.—Magoun and Copeland (1998) defined natal dens as the location of birth, maternal dens as sites other than the natal den where cubs are located prior to weaning, and rendezvous sites as locations used after weaning. In those cases where we eventually confirmed reproduction, we estimated parturition date based on midpoint between first date located in a concentrated area and date of the location made previous to the concentration of locations (O’Pezio et al. 1983). When a female denned while wearing a GPS collar we used the first date that she remained at the natal den site for several consecutive days as the parturition date. When we located the den of an unmarked

female, we estimated parturition based on tooth eruption of the cubs (C. Long, The Wolverine Foundation, unpublished data). We estimated the dates that different den types were used based on our estimated parturition date and weaning at 10 weeks (Iverson 1972).

Natal dens.—When telemetry data indicated a potential den, we visited the site, marked the potential natal den entrance, and measured snow depth. We classified only those sites that eventually produced evidence of cub presence as natal dens. We also located the den of an unmarked female by following her tracks back to the den and subsequently documenting a litter. We classified this site as a natal den based on extended use over a long period as indicated by an extensive network of tunnels and numerous scat piles at the site. We visited sites verified as natal dens during summer, when we recorded detailed habitat characteristics including elevation, macro-aspect, habitat type (Despain 1990), and structural components of the den.

Maternal dens and rendezvous sites.—We recorded habitat characteristics of maternal den and rendezvous sites during attempts to document litter size or capture and radio-mark juvenile wolverines. Only those sites where we observed cubs or tracks of cubs were classified as maternal dens or rendezvous sites. Distinction between maternal den and rendezvous site was based on our estimated date of parturition and the age of the cubs at the date when the site was used. We considered sites used prior to an estimated age <70 days maternal dens and those used at ≥ 70 days rendezvous sites.

Maternal food habits.—We collected scats and information on food items (remains) present at den and rendezvous sites when visiting these sites. We were also able to observe females with cubs as they foraged on a few occasions. The period of maternal care lasts through at least early fall and may be critical to successful recruitment. Thus far, we have not made extensive efforts to document maternal food habits. In the future, we may attempt to intensify our efforts.

RESULTS

Reproductive Parameters

Proportion of females reproducing.—We captured 17 female wolverines between January 2002–May 2007 and monitored them for reproduction during 40 female-years. Six reproductions occurred in 23 adult-female-years for a total of 0.26 litters/adult female/year and an annual average of 0.34 ($n = 6$ yrs, 90% CI = 0.07–0.62) litters/adult female (Table 1). Only 4 of the 12 females that were nulliparous at their first capture were estimated to be older than the minimum possible age; when we assigned these 4 females their minimum possible age, the sample size of adult-female-years was reduced from 23 to 20; this yielded a maximum of 0.30 reproductions/adult female/year.

Age at first reproduction.—We monitored 4 females from birth, F405, F421, F133 and F135. F405 and F421 were born in the Teton Range during February 2004 and neither reproduced at 1 or 2 years of age. F405 died during mid-December 2006, 2 months prior to her 3rd birthday; her carcass is awaiting necropsy and will be examined for reproductive condition. F421 did not yield any indication of localizing at a den site during the

Table 1. Proportion of adult female wolverines reproducing (litters/adult female/year), annual birth rate (cubs/adult female/year), and recruitment rate (cubs alive 1 March the year after birth/adult female/year) in the Greater Yellowstone Area of Idaho, Montana, and Wyoming, 2002–2007.

Year	No. adult females monitored ^a	No. adult females reproduced ^a	Proportion adult females reproduced ^a	No. cubs	Annual birth rate	Cubs recruited	Recruitment rate
2002	2	2	1.00	2	1.00	.	.
2003	3	0	0.00	0	0.00	0	0.00
2004	3	2	0.67	3	1.00	3	1.00
2005	4	1	0.25	1	0.25	0	0.00
2006	4	0 ^b	0.00	0 ^b	0.00	1 ^b	0.20
2007	7	1	0.14	1	0.14	.	.
Total ^c	23 or 15	6	0.26	7	0.30	4	0.27
Annual mean (SE) ^c	6 or 4 yrs		0.34 (0.17)		0.40 (0.19)		0.30 (0.24)

^a Adult females only, i.e., ≥ 3 years of age at 1 March of reproductive year.

^b We documented 1 additional cub of an unmarked female during 2006 by tracking the female back to a natal den site. We did not use this observation in estimates of reproductive frequency or annual birth rate because there was no possibility of documenting a lack of reproduction (Persson et al. 2006). However, we did use this observation in our estimate of recruitment rate.

^c Sample size for recruitment was lower than other parameters.

denning season of 2007, thus it appears that she did not reproduce at 3 years of age. F133 was born in the Gallatin Range during 2006 and did not reproduce at 1 year of age. F135 was born in the Gravelly Range during 2007.

A total of 12 females had not given birth by the time we first captured them (including 3 known-age females above except F135), and we were able to observe their reproductive status over 1–5 consecutive years. Using minimum possible age of these individuals, i.e. assuming an individual was born during the spring prior to our first capture of her, 12 of 12 females (100%) did not reproduce at 1 year of age, 8 of 9 (89%) did not reproduce at 2 years of age, 4 of 5 (80%) did not reproduce at 3 years of age, and 1 of 2 (50%) did not reproduce at 4 or at 5 years of age. The assumption of minimum age at first capture could only bias age at first reproduction to be lower than it actually is. Overall, these data suggest that first reproduction at <4 years of age may be uncommon in GYA. Also, at least some individuals do not reproduce until ≥ 6 years of age.

Litter size.—We confirmed the presence of 8 cubs born to 5 females. Mean litter size was 1.1 cubs ($n = 7$ litters). We were not able to identify the sex of 3 cubs; thus cub sex ratio was 4F:1M. Two adult females, F401 and F107, died during January 2003 or February 2004 and each contained 4 embryos *in utero*. Sex ratio was 1F:3M for the female that died in February (N. Anderson, Montana Department of Fish, Wildlife and Parks, personal communication). We were not able to determine sex ratio in the case of the female that died in January.

Annual birth rate, interbirth interval, and recruitment rate.—We documented a total of 7 cubs born to 5 females during 23 adult-female-years for a total annual birth rate of 0.30 cubs/adult female/year (Table 1, see footnote b). Annual birth rate ranged from 0.00–1.00 cub/adult-female, and averaged 0.40 cubs/adult-female ($n = 6$ yrs, 90% CI = 0.08–0.72).

Mean inter-birth interval was 1.5 years ($n = 2$, Table 2). If we assume that 1) *in utero* litters would have been born if F401 and F107 had survived, 2) F107 and F121 had both given birth

Table 2. Inter-birth intervals of wolverines in the Greater Yellowstone Area of Idaho, Montana, and Wyoming, 2002–2007.

Year	Wolverine					
	F401	F404	F105	F107	F121	F134 ^a
2002	Litter ^b	Litter ^b	.	.	.	.
2003	Litter ^c	No litter	No litter	No litter ^b	.	.
2004	.	Litter	Litter ^d	Litter ^c	.	.
2005	.	No litter	Litter	.	No litter ^b	.
2006	.	No litter	No litter	.	No litter	Litter
2007	.	No litter	No litter	.	Litter	.

^a Unmarked female.

^b Reproduced prior to our first capture.

^c *In utero* litter during late January or mid-February of a female that died before giving birth.

^d First litter.

the year prior to our first capture of them, and 3) F404 and F105 will give birth during 2008 after skipping 3–4 years, the resulting mean interbirth interval would be 2.3 years ($n = 7$, Table 2). All of these assumptions, if erroneous, would bias the estimated interbirth interval lower than it actually is, thus 2.3 years could be considered a minimum interbirth interval.

Four cubs known to be alive 1 March of the year following birth were produced in 15 adult-female-years, resulting in a total recruitment rate of 0.27 cubs/adult female/year (Table 1). Annual recruitment rate ranged from 0.00–1.00 cubs/adult female, and averaged 0.30 cubs/adult female ($n = 5$ yrs, 90% CI = 0.00–0.69).

Timing of Reproductive Events and Maternal Habitat

Parturition date.—We documented the presence of litters of radio-marked females on 6 occasions. Telemetry or GPS collar data indicated that use of 2 of the natal dens began between 14–21 February and use of other natal dens began on 23 February, 16 February, between 15 January–12 February, and between 31 January–10 February. We estimated one parturition date based on tooth eruption of the cub at capture to be 8 March. Therefore, mean parturition date was 16 February (Fig. 2). Parturition could have occurred over as few as 20 days (12 Feb–1 Mar) or as many as 60 days (15 Jan–15 Mar).

Natal den habitat.—We located 5 natal den sites used by 4 females (Photos 1–6). Elevation at these 5 natal dens ranged from 2,396–2,822 m (7,860–9,259 ft), and macro-aspect was north at all sites. Snow depth ranged from 1.5–3.5 m at our first visit (23 Feb–3 Mar for radio-marked females, 21 April for the unmarked female). All natal dens were located in avalanche debris, and the primary structural component was logs approximately 10–100 cm (4–40 inches) diameter at breast

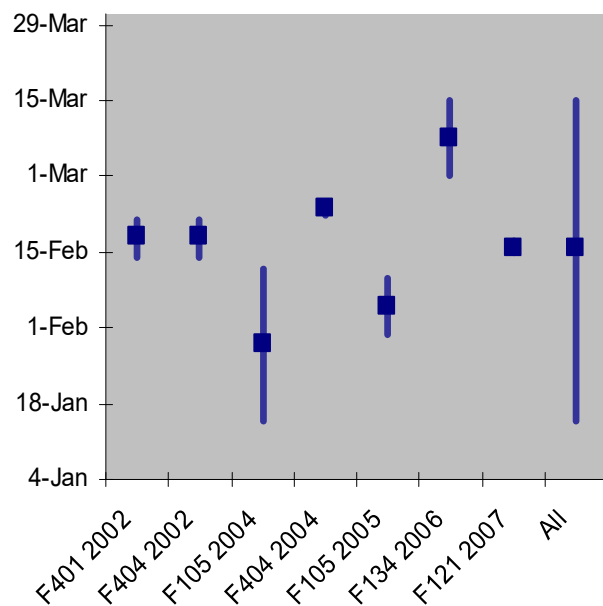


Figure 2. Estimate and range of possible parturitions dates for wolverines in the Greater Yellowstone Area of Idaho, Montana, and Wyoming, 2002–2007.

height. Down logs of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) were common structural components at 2 sites. One site consisted of Douglas fir (*Pseudotsuga menziesii*), and another was composed of Engelmann spruce, whitebark pine (*Pinus albicaulis*), and subalpine fir. The 2007 den was also in an avalanche chute and associated with woody debris, but we have not determined the specific characteristics yet. Boulder talus was located <500 m from all 5 natal dens. Four of 5 (80%) natal dens were located in alpine habitats, near timberline, where boulder talus and open meadows were interspersed with forested areas (Photos 1–4 and 6). The fifth natal den was located near the bottom of a major drainage in an area of mature Douglas fir (Photo 5); this site was <2 km from habitat similar to the other natal dens. We did not document the exact location of 2 additional natal dens used in the Teton Range during 2002, however we were able to acquire some general information on macro-site characteristics based on the telemetry locations. One of these natal den sites was in designated wilderness at approximately 2,200 m elevation (7,200 ft.) in heavily forested area of mixed conifer. This site was >4 km from alpine timberline. The second was likely at 2,500–2,750 m elevation in a steep canyon of Grand Teton National Park which faced north. Three of 5 natal dens were located in designated wilderness. One den was in a wilderness study area where motorized use was allowed during winter but was most likely absent due to difficult access. One den was located in an area open to motorized use during winter and we documented a small amount of snowmobile use near the natal den (Photo 6). Four of 5 natal den sites were used through at least late April.

Maternal den sites.—Based on our estimated birth dates, natal dens were used past the time of weaning in 2 cases and probably until within a week of weaning date in 2 more cases. Thus use of maternal dens was minimal for these 4 reproductive events. GPS collar data suggests that the 5th natal den was vacated during early March (cub age of 3 weeks) when use of a maternal den approximately 300 m from the natal den site initiated. We will investigate the habitat characteristics at this potential maternal site in the near future.

Rendezvous site habitat.—We located 9 rendezvous sites where we observed cubs at the site or found evidence of use by cubs. Wolverines used these sites between 29 April–2 July. These rendezvous sites were 2.3–14.7 km from their respective natal den sites. Eight of 9 (89%) rendezvous sites were located in alpine habitats, near timberline, where boulder talus and open meadows were interspersed with forested areas (Photos 7–10). These sites were at 2,597–2,865 m elevation (8,520–9,400 ft). Habitat at the other rendezvous site differed considerably as it was at a lower elevation (2,195 m) in a heavily forested mixed conifer stand (primarily subalpine fir interspersed with a few small lodgepole pine) that was >4 km from timberline (Photo 11). The primary structure of these rendezvous sites was large boulders (44%), logs in avalanche debris (33%), or down logs (22%; Photos 7–11). Snow was present at all sites when the wolverines used them except the one used during July. In most

cases there were multiple tunnels through the snow associated with the structure, and these tunnels appeared to be the result of the structure rather than extensive excavation by wolverines.

Maternal food habits.— We found the remains of ungulates, either moose (*Alces alces*), elk (*Cervus elaphus*), or mule deer (*Odocoileus hemionus*), at all natal den sites, and evidence of wolverines feeding on yellow-bellied marmots (*Marmota flaviventris*) at one natal den site. We found the remains of yellow-bellied marmots at 5 of 9 rendezvous sites and either elk, mule deer, or mountain goat (*Oreamnos americanus*) remains at 6 of 9 rendezvous sites. On 16 June 2004 we located a young elk calf that had been killed by F105 within a few hours prior to our arrival (Photo 9). F105 had removed the head and one rear leg and transported them approximately 0.75 km to the rendezvous site. We filmed her as she attempted to take the remainder of the carcass to the rendezvous site.

DISCUSSION

Reproductive Parameters

Studies of wolverine carcasses from North America have provided a significant amount of data related to reproduction (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). These studies suggest that approximately 40% of female wolverines are capable of giving birth at 2 years of age and that litter size averages approximately 3.4 cubs. However, estimates from carcasses are subject to error associated with the cementum annuli aging technique, which may be significant in the case of wolverines (J. Persson, unpublished data). In addition, while the vast majority of sexually mature females may be pregnant (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988), reproductive data from field studies indicates that most females do not produce a litter in a given year (or at least maintain one through weaning; Magoun 1985, Copeland 1996, Persson et al. 2006). Resorption or early litter loss may be adaptive for wolverines (Inman et al. 2007b) and fairly common (Banci and Harestad 1988, Persson et al. 2006). Therefore wolverine

carcass studies likely underestimate age at first reproduction, overestimate litter size, and generally overestimate the realized reproductive rate of the species. In the case of wolverines, accurate information may depend on field studies, and monitoring known-age females (captured at dens as cubs) is particularly important.

Data on first-litters born to known-age females are limited to one study in Scandinavia where Persson et al. (2006) monitored females from birth and reported that 0 of 11 reproduced at 2 years of age, 3 of 10 reproduced for the first time at 3 years of age, and 2 wolverines did not reproduce until 4 years of age. This resulted in an average age of first reproduction of 3.4 years (Persson et al. 2006). Our data suggest that average age at first reproduction in GYA is at least 3 years, however, it appears quite possible that it could be higher. GYA is at the southern extent of the wolverines global distribution and is home to a greater diversity of ungulate and carnivore species than most other areas where wolverines have been studied. While it seems intuitive that this situation could be beneficial to the scavenging habits of the wolverine, we found no evidence that reproductive rates in GYA are greater than in other regions. All of our estimates of reproductive parameters (litter size, annual birth rate, inter-birth interval, and recruitment rate) indicate that the reproductive capability of wolverines in GYA may be less than that documented by other field studies, including those from North America where our sample sizes were similar (Table 3). Most of these studies occurred at more northern latitudes where home ranges are smaller than in GYA (Magoun 1985, Banci and Harestad 1988, Wedholm 2006, Copeland and Yates 2006, Inman et al. 2007a). Perhaps food resources for wolverines are more abundant in these areas than in GYA (Sandell 1989). Although reported reproductive rates from North America likely do not differ statistically due to their small sample sizes, our lower estimates combined with the relatively large home ranges of GYA wolverines suggest that caution is warranted when using data from other areas to represent reproductive rates in GYA. Appropriate reproductive parameters for wolverines in GYA are necessary for population

Table 3. Location, estimates, and sample sizes reported for wolverine age at first reproduction (years), litter size, annual birth rate (cubs/adult female/year, n = adult-female-years), inter-birth interval (years), and recruitment rate (cubs alive on 1 Mar of year following birth/adult female/year, n = adult-female-years).

Location	Reference	Age at first reproduction ^a	n	Litter size	n	Annual birth rate	n	Inter-birth interval	n	Recruitment rate	n
Scandinavia	Pulliainen (1968)	.	.	2.5	161	.	.	.	.	.	.
Scandinavia	Persson et al. (2006)	3.4	<10	1.9	74	0.74 ^c	83	1.4	30	0.46	71
Alaska	Magoun (1985)	.	.	1.8	5	0.69 ^b	13	1.5	2	.	.
British Columbia	Lofroth (2001)	.	.	.	.	0.50	20	.	.	.	.
British Columbia	Krebs and Lewis (1999)	.	.	2.0	3	0.43	14	1.0	2	.	.
NW Montana	Copeland and Yates (2006)	.	.	2.0	2	.	.	.	.	.	.
Idaho	Copeland (1996)	.	.	2.0	4	0.89 ^c	9	1.3	3	.	.
Yellowstone	This study	>3	2	1.1	7	0.30 ^c	23	2.3	7	0.27	15

^a Known-age females only.

^b Adult-female-years included those ≥ 2 years old.

^c Adult-female-years included those ≥ 3 years old

modeling and development of effective conservation strategies, including allowable mortality. Therefore it remains important to monitor known-age females and gather additional data on reproductive parameters in GYA. The need for GYA specific information is further warranted since maintaining reproductive capacity in this region may be more critical than usual due to the island-like nature of primary habitat in the conterminous U.S. and the dependence of a wolverine metapopulation on successful dispersal (Cegelski et al. 2006, Brock et al. 2007).

Development of an appropriate dataset on wolverine reproductive rates requires long-term research projects. Even though we have made extensive capture efforts over a vast effective area (6 years, 94 traps and 7,984 trap-nights over approximately 9,000 km²), low annual samples of adult females have limited our ability to document reproductive parameters. Although we have captured 17 female wolverines, many were young (1–2 yr) during the reproductive seasons that we have monitored them and several died prior to reproducing. In addition, the 2–7 adult females monitored during each of the 6 years of study have not reproduced every year and some have died. As a result, very few litters have been born and the possibility of monitoring known age females through their first reproduction has been restricted. We are currently limited to a sample size of 3 known-age females, one is 3 years of age (but has dispersed outside of our permitted research area), another is 1 year of age, and the third was captured this spring (a fourth known-age female died in an avalanche during December 2006 at 2.75 years of age). Six of 7 females that we are currently monitoring are now adults (≥ 3 yrs on 1 March 2007). With reasonable survival, our chances of capturing known age cubs and amassing a more significant dataset for all reproductive parameters is increasing. A dataset for age at first reproduction from known age females that is equivalent to that published from Scandinavia (Persson et al. 2006) will likely require an additional 5 years of effort. We estimate that this length of time would allow us to increase sample sizes for age at first reproduction and inter-birth interval to 10, litter size, parturition date, and natal den habitat to 20, and annual birth rate and recruitment rate to 50 adult-female-years. We have shifted our efforts to focus more specifically on reproduction, relying on capture of cubs during the spring and targeted captures of females. We have not at present secured funding to continue to monitor these females past spring 2008.

Maternal Habitat

Thirteen of 16 natal den and rendezvous sites (81%) were located in alpine habitats, near timberline where boulder talus and open meadows were interspersed with forested areas, and where snow was typically present through at least June. These 13 sites occurred within a 400 m elevation band (2,500–2,900 m, 8,200–9,500 ft), and, with the exception of 1 rendezvous site, at northern aspects (301–68°). Natal dens were all associated with structure from avalanche debris, whereas rendezvous sites occurred in avalanche debris, under large boulders, and under down logs. Natal den sites were highly secure; deep snow-cover and numerous small tunnels and chambers under the tangle of logs and branches made access by anything larger than a wolverine difficult. Two natal den sites that were used a total of

4 times in Idaho (Magoun and Copeland 1998) were located in cirque basins above 2,500 m (8,202 ft), on northern aspects, and under snow-covered boulder talus with timber nearby. While the den structure differs between GYE and Idaho, the general habitat used in both studies was similar. Extrapolation of these denning habitat characteristics (elevation) to locations outside of GYA would benefit from accounting for the effect of latitude on the elevation at which alpine timberline occurs. This can be done relatively easily (Brock and Inman 2006).

February appears to be the primary period of wolverine parturition in GYA. The dates we observed parturition were similar to those observed in Idaho (Copeland 1996). Births during late February and early March are common at more northern latitudes (Inman et al. 2007b). The life history strategy of the wolverine seems to be based on exploiting a relatively marginal niche where limited food resources, especially during winter, may be spread over a large area (Persson 2005, Inman et al. 2007a). Timing and success of parturition may, in part, be related to the potential for a female to cache sufficient food stores over-winter to supply the energetic demands of lactation (Inman et al. 2007b). We found ungulate remains at all natal dens and most rendezvous sites. Wolverine distribution coincides with the presence of snow during late spring (Aubrey et al. 2007), and this could be related to their ability to store food caches for extended periods in these snowy areas and then utilize them to fuel lactation. As temperatures warm and snow melts, these caches become increasingly exposed to other species and deterioration. But, at the same time, small prey such as rodents are emerging from hibernation or exposed. Even with the limited amount of effort we exerted to obtain information on maternal food habits, marmots also appeared to be an important food item, as they were in British Columbia (Lofroth et al. 2007). Selection of denning habitat by wolverines in GYA is likely related to the interaction of at least 4 factors, 1) the presence of deep snow and complex structures to protect newborns from potential predators and the severe temperatures that occur during the parturition period, 2) the ability to cache ungulate carrion in areas that retain snow for long periods, 3) structure that inhibits other spring scavengers (e.g., bears) from pilfering caches, and 4) proximity to marmot colonies.

We quietly approached 5 natal dens on skis early in the period of use (12–44 estimated days of kit age) and none were abandoned. In two cases, the female was definitely aware of our presence, and it is highly likely that the female was aware of our presence in all cases. In one case the depth of snow covering a portion of the natal den was <25 cm deep and we accidentally created a small hole in the snow with a ski pole while attempting to flag the location of the den. GPS collar data suggests that the female may have moved to a maternal den site approximately 300 m away a minimum of 5–7 days after our visit. During this 5–7 day period, there was a light amount of snowmobile use near the dens (Photo 6). It is unknown whether the move to the maternal den was the result of our slight alteration of the den, the presence of snowmobile activity, or neither. Females did not abandon natal dens in Alaska or Scandinavia when researchers approached (Magoun 1985, Persson et al. 2006). However, 6 of 7 natal dens from this study occurred in areas without motorized use, i.e., designated wilderness, areas inaccessible by vehicle, or

national park. We have not yet examined the availability of denning habitat within motorized use areas. Much of the habitat that meets the elevation and aspect characteristics of our natal den sites likely falls outside of motorized areas, and selection of natal den sites could be a result of habitat characteristics other than the types and levels of human use occurring nearby. On the other hand, many authors have suggested that refugia are important for wolverine reproduction (Banci 1994, Magoun and Copeland 1998), and our observations certainly do not suggest otherwise at this time.

MANAGEMENT IMPLICATIONS

Wolverine reproductive capacity is low relative to most carnivores, and reproductive rates of wolverines in GYA appear to be as low as or possibly lower than reported from other regions. The wolverine's life history strategy in GYA appears to be based on occupation of a marginal niche, and their ability to compensate for increased mortality is limited (Krebs et al. 2004, Persson et al. 2006, Inman et al. 2007a). Given this inherent vulnerability, limiting human-induced mortality, especially that of adult females, is an important management consideration. Providing adequate resources and limiting additive, human-caused, energetic expenditure may also be critical for successful reproduction and population persistence (e.g., adequate prey base, unencumbered access to food sources, and secure maternal habitat). The importance of doing so in the conterminous U.S. may be exacerbated by the fact that wolverine habitat occurs in island-like fashion and dispersal is likely key to long-term persistence (Cegelski et al. 2006, Brock et al. 2007). While successful reproduction is likely critical in all habitats used by a metapopulation of wolverines in the conterminous U.S., reproduction in smaller mountain ranges that are in-between "regional population centers" (RPCs; Brock et al. 2007) may be of greatest importance given their increased likelihood of accomplishing genetic exchange among RPCs. Development of successful management strategies based on appropriate levels of mortality, including harvest, depends on accurate estimates of reproductive rates. Obtaining this information for wolverines is logistically difficult, expensive, and will depend on adequate funding for a long-term study. The cost of acquiring these data could be reduced with access to designated wilderness areas via helicopter for short periods of time during a couple of weeks in March and May. Granting this access over a relatively brief interval (5–10 years) could improve the long-term persistence of a species that is an integral component of wilderness.

Similar to other reports from North America, wolverines in GYA placed natal dens and rendezvous sites in alpine habitats, near timberline, where boulder talus and open meadows were interspersed with forested areas. The majority of sites occurred within a 400 m elevation band (2,500–2,900 m, 8,200–9,500 ft) at northern aspects (301–68°) and were used during February–June. Natal dens were all associated with structure from avalanche debris, whereas rendezvous sites occurred in avalanche debris, under large boulders, and under down logs. Structure under deep and persistent snow cover along with proximity to marmot colonies may be key in selecting these

sites. Our den sites and these habitat characteristics in general are often associated with areas where motorized access is limited or prohibited. It is not clear at this point whether wolverines are selecting maternal habitat based on a lack of human activity. However, due to the inherently vulnerable life history strategy of the wolverine, caution is warranted with regard to factors that could influence reproductive success. Efforts to provide secure maternal habitat may be important to the persistence of wolverines in GYA.

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Photo 1. Wolverine F105's 2005 natal den site, Spanish Peaks, Montana, USA. Photos taken 3 March and 17 July, 2005.



Photo 2. Wolverine F105's 2004 natal den site, Spanish Peaks, Montana, USA.



Photo 3. Wolverine F134's 2006 natal den site, Gallatin Range, Montana, USA. Photos taken 21 April and 4 September, 2006.



Photo 4. Extensive structure of wolverine F134's 2006 natal den site, Gallatin Range, Montana, USA. Note person in picture directly above for scale and log that is above snow in Photo 3.



Photo 5. Wolverine F404's 2004 natal den site, Teton Range, Wyoming, USA. This site occurred at a lower elevation and in a more densely forested area than most natal dens. Photos taken 23 Feb and 15 July, 2004

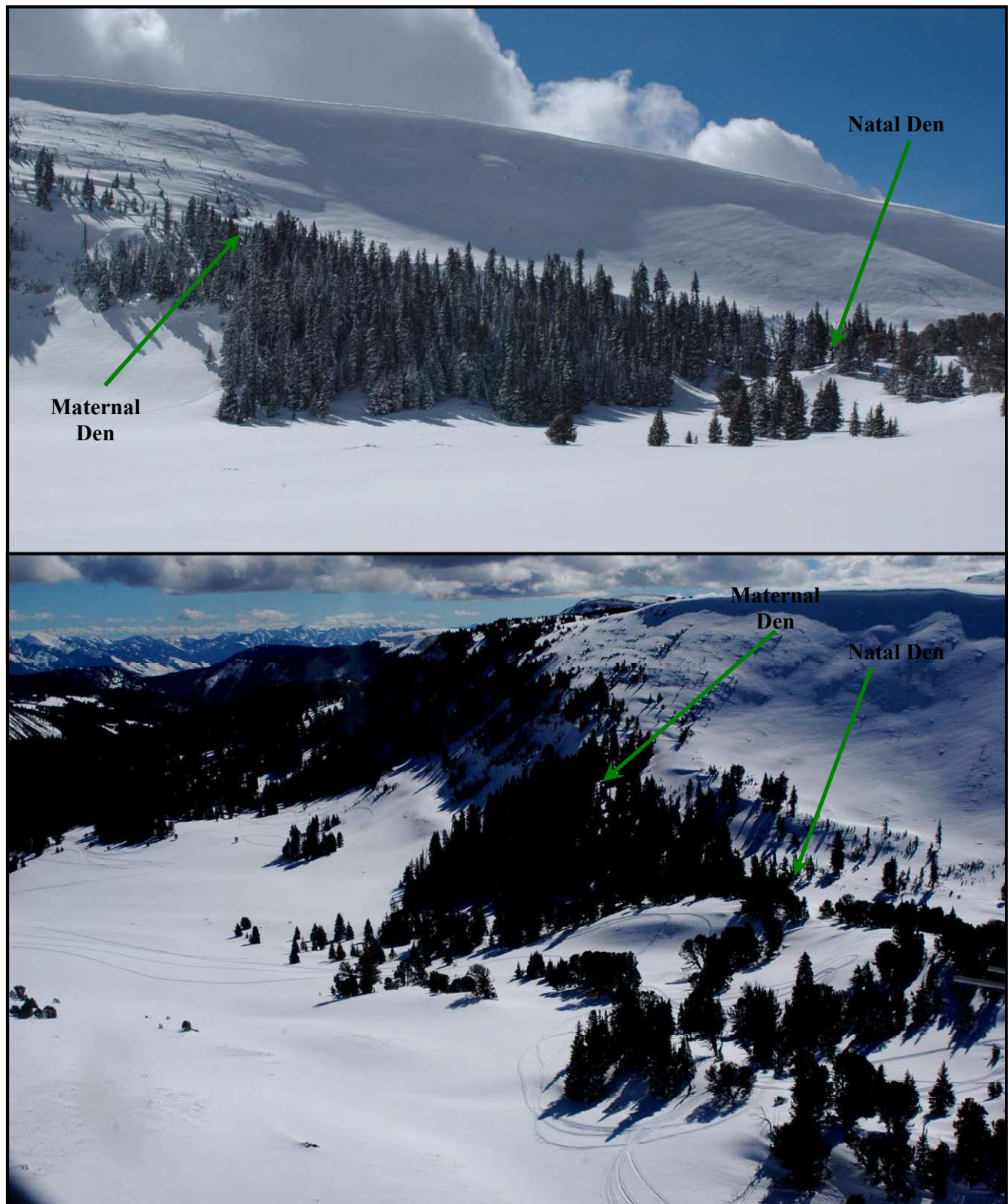


Photo 6. Wolverine F121's 2007 natal and maternal den sites (top and bottom photos) and a light amount of recreational snowmobile use near the dens (bottom), Gravelly Range, Montana, USA. Photos 28 February and 6 March, 2007.



Photo 7. Wolverine F105's 29 April, 2005 rendezvous site, Spanish Peaks, Montana, USA (note person in bottom photo between the large boulders for scale). Photos taken 29 April and 19 July, 2005.



Photo 8. Wolverine F105's 2 May, 2004 avalanche debris rendezvous site, Spanish Peaks, Montana, USA. Photos taken 2 May and 30 July, 2004.



Photo 9. Wolverine F105's 16 June, 2004 rendezvous site, Spanish Peaks, Montana, USA. She had killed an elk calf that morning and we filmed her as she cached it under a large boulder.



Photo 10. Wolverine F134's 18 May, 2006 rendezvous site, Gallatin Range, Montana, USA. Photos taken 18 May and 3 September, 2006.



Photo 11. Wolverine F401's 24 May, 2002 rendezvous site, Teton Range, Wyoming, USA. Photos taken 24 May and 2 June, 2002. This site was at a lower elevation and in a more heavily forested area than most other rendezvous sites. Numerous subalpine fir trees had been blown down at the site.