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REPRODUCTIVE CHARACTERISTICS OF FEMALE WOLVERINES (*GULO GULO*) IN SCANDINAVIA

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We studied reproduction of 56 female wolverines (*Gulo gulo*) in 2 areas of northern Scandinavia. Minimum average age at 1st reproduction was 3.4 years. Mean proportion of females ($\geq$3 years old) reproducing was 0.53 (95% confidence interval [*CI*] = 0.43–0.63, n = 94), and the annual mean was 0.58 (95% *CI* = 0.35–0.80, n = 83). Mean annual birth rate was 0.74 (95% *CI* = 0.33–1.14, n = 83) young per female ($\geq$ 3 years old). Mean size of 74 litters was 1.88 (95% *CI* = 1.68–2.07, range = 1–4). Examination of our data suggests that female wolverines have low productivity and low capacity to compensate for increased mortality. Therefore, wildlife managers should consider wolverine demographics, especially mortality of adult female wolverines, when developing and implementing conservation policies and harvest regulations.

Key words: birth rate, carnivore, *Gulo gulo*, litter size, mustelid, recruitment, reproduction, Scandinavia, wolverine

Animal populations are dynamic because of variation in rates of reproduction, survival, immigration, and emigration. Age at 1st reproduction, birth rate, and age-specific differences in productivity interact to determine a population's reproductive rate. In turn, reproductive rates are strongly influenced by environmental factors, including food abundance, climate, and parasite load (Bronson 1989; Roff 1992; Stearns 1992). In Scandinavia, predation by wolverines (*Gulo gulo*) on semi-domestic reindeer (*Rangifer tarandus*) and free-ranging domestic sheep (*Ovis aries*) conflicts with livestock husbandry (Bjärvall et al. 1990; Landa et al. 2000b). Wolverines are protected in Sweden, although the population is managed through legal harvest in Norway (Sæther et al. 2005). In North America, wolverine management issues include regulating trapper harvest, preventing human disturbance at denning sites, and mitigating for habitat loss and fragmentation (Copeland 1996; Krebs et al. 2004).

Compared with other large carnivores, knowledge of wolverine reproduction is poor (Kucera and Zielinski 1995; Landa et al. 2000a). Current knowledge about wolverine reproductive biology is mainly based on in utero examination of harvested wolverines (Banci 1994) and observations of captive wolverines (e.g., Mead et al. 1993). However, observations from a limited number of radiocollared individuals have provided some insight on reproductive characteristics in wild wolverines (Copeland 1996; Magoun 1985). Current management issues and lack of information emphasize that sound management policies for wolverines require more reliable data on demography, for example, reproductive patterns.

Female wolverines attain sexual maturity at about 15 months, but the proportions of females that are pregnant at the age of 2 years is variable (Banci and Harestad 1988; Liskop et al. 1981; Rausch and Pearson 1972). This variation may in part be due to uncertainties in cementum analysis as an exact aging method for wolverines (Banci 1982; Landa and Skogland 1995). Pregnancy rates determined from reproductive tracts of harvested wolverines (Banci 1994) suggest that most females (>2 years old) mate every year. However, sparse information from radiocollared wolverines (Copeland 1996; Magoun 1985) indicates that the proportion of females in the population that successfully rear young is lower than the proportion of pregnant females in the population.

This study involved monitoring of radiocollared free-ranging wolverine females. We determined age at 1st reproduction in females monitored from birth, proportion of females reproducing, birth rates, litter size, sex ratio of juveniles, and recruitment of juveniles to 1 year of age.

MATERIALS AND METHODS

Study areas.—This study was conducted in and around Sarek National Park in Norrbotten County in northern Sweden (Kvikkjokk: 67°00′N, 17°40′E) and in the southeastern part of Troms County in northern Norway (Dividalen: 68°50′N, 19°35′E). Study areas were 7,000 km^2 and 2,500 km^2, respectively. Mean temperatures were

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−13°C in winter (January) and 14°C in summer (July) at both areas. Annual precipitation ranged from 500 to 1,000 mm in both areas (Påhlsson 1984; Ryvarden 1997). The ground was mostly snow-covered from October to May. Both areas were characterised by deep valleys, glaciers, and high alpine plateaus with peaks ranging from 1,700 to 2,000 m in elevation. The valleys were dominated by mountain birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*). Norway spruce (*Picea abies*) also was abundant in Sarek (Grundsten 1997). Mountain birch formed the tree line in both areas and reached a maximum of 600–700 m above sea level. (Grundsten 1997; Ryvarden 1997). Both study areas constituted parts of reindeer herding districts where semidomestic reindeer were herded by indigenous Sámi people. Free-ranging domestic sheep grazed during summer in the western part of the Troms area. The approximate densities of wolverines were 1.4/100 km^2 in Sarek and 1/100 km^2 in Troms (see methods, Landa et al. 1998).

Animal capture and monitoring.—We radiocollared and monitored females from 1993 to 2002. We captured juveniles at rendezvous sites (sites where young were left while the female foraged, after abandonment of the natal den) from early May to early June (i.e., when young were 2–3 months old) in 1993–2002. Adult females were captured at rendezvous sites or were darted from a helicopter. The wolverines were anesthetized with xylazine and ketamine (Arnemo et al. 1998) or medetomidine and ketamine (Arnemo et al. 2004, Biomedical protocol for free-ranging wolverines (*Gulo gulo*) in Scandinavia, at http://www.wolverinefoundation.org/research/bpfrws04.pdf.). Young were initially equipped with transmitters attached to the fur (31–34 g, Telonics Model 055, Mesa, Arizona) and later with collar-mounted radiotransmitters (150–200 g; Telonics Model 315) as body mass increased, in Sarek from 1993 to 1996. From 1996, all young were equipped with intraperitoneally implanted transmitters (30–90 g, Telonics Imp/210/L, Imp/300/L, or Imp/400/L). Adult wolverines were equipped with either intraperitoneally implanted transmitters (30–90 g, Telonics Imp/210/L, Imp/300/L, or Imp/400/L) or collar-mounted radiotransmitters (150–200 g, Telonics Model 315). The study was approved by the Animal Ethics Committee for northern Sweden, Umeå, and by the Animal Ethics Committee of Norway. Procedures for capture and handling of wolverines followed the guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

We radiotracked wolverines weekly during the denning season (mid-February to the end of April) by plane, complemented with additional ground-based telemetry, to find dens. A female was considered reproducing when she was found repeatedly at the same site during the denning season and visits on the ground confirmed the existence of a den (Magoun and Copeland 1998). In no case did ground inspections result in a female abandoning a den. The occurrence of denning is a conservative index of reproduction because some females may lose their young early after parturition and abandon their dens. The presence and number of young were determined from early May to early June by snow tracking, visual observation with spotting scope, capturing family groups, or a combination of these. Consequently, we provide minimum estimates of birth rates and litter size.

We measured reproduction as the proportion of females that reproduce each year, annual birth rate, mean individual birth rate, litter size, and recruitment rate. The proportion of females (3 years old) that reproduce each year was based on confirmed denning and was estimated for all females pooled together as well as on the mean annual proportion from years when >10 females were monitored (i.e., 1997–2002). We excluded the 1st year of monitoring for females located and captured by searching known natal den sites ($n = 34$ female years), to avoid a positive bias in reproductive parameters. Annual birth rate was defined as the number of young per telemetered female (3 years old) in May–June. This estimate gives more weight to animals that were monitored longer. Individual birth rate is the mean of each individual female's birth rate (3 years old) for females monitored more than 1 year. This estimate gives equal weight to each female. Recruitment rate (Sæther et al. 2005) is the number of young per female (3 years old) that were known to be alive at the age of 1 year (assuming 1st of March as date of birth). Means are presented with 95% confidence intervals (95% *CI*s). We used chi-square tests to test for differences in sex ratio among young, and statistical significance was inferred at $P \leq 0.05$.

Results

Animal capture.—We captured and telemetered 56 adult (2 years old) female wolverines (37 in Sarek and 19 in Troms) during the study period (1993–2002 in Sarek; 1996–2002 in Troms). We monitored adult females during a total of 141 individual reproductive seasons (105 in Sarek and 36 in Troms), recording the production of 88 litters.

Age at 1st reproduction.—None of 11 females monitored from birth reproduced at the age of 2 years. Three (30%) of 10 females reproduced for the 1st time at the age of 3 years, and 4 (67%) of 6 females reproduced at the age of 4 years (2 of which were for the 1st time). Overall, 5 (83%) of 6 females had reproduced at least once by the age of 4 years. Finally, 2 (67%) of 3 females reproduced at the age of 5 years. Both of the reproducing females had reproduced once before, whereas the nonreproducing female had never reproduced during the study. We lost radiocontact with 1 female at the age of 2 years but recaptured her when she reproduced at age 4. The average age of 1st reproduction among 6 females monitored to 1st reproduction was 3.4 years.

Reproductive rates.—When the 1st year of monitoring was excluded and all female years were pooled together, the total proportion of females reproducing each year was 0.53 (95% $CI = 0.43–0.63$, $n = 94$) Furthermore, the mean annual proportion of females reproducing during the period 1997–2002 was 0.58 (95% $CI = 0.35–0.80$, $n = 83$) and ranged from 0.29 to 0.82 (Table 1). Based on denning behavior, 15 (30%) of 50 litters were lost before June (33%, $n = 39$, in Sarek; 18%, $n = 11$, in Troms). Thirty-seven percent ($n = 94$) of female years produced young that survived to weaning (i.e., to mid-May). The mean annual birth rate was 0.74 young per female (95% $CI = 0.33–1.14$, $n = 83$; Table 1). The individual birth rate for females monitored for at least 2 years (mean 3.2 years) was 0.71 young per female (95% $CI = 0.40–1.01$, $n = 22$). The birth rate for individuals varied from 0 to 2.5 young per female.

In Sarek, 33 young (19 females and 14 males), known to survive to 1 March of the following year, were produced in 71 female years. This represents a recruitment rate of 0.46 young per female (95% $CI = 0.22–0.70$) that survived to the age of 1 year (0.27 females; 95% $CI = 0.10–0.43$ and 0.20 males; 95% $CI = 0.06–0.33$). Furthermore, the mean annual recruitment was 0.40 young per female (95% $CI = 0.15–0.65$, $n = 68$) to the age of 1 year (0.23 females; 95% $CI = 0.05–0.41$;

and 0.2 males; 95% *CI* = 0.07–0.31). Too few juveniles were monitored to the age of 1 year in Troms, because of lost radiocontact, to be included in our recruitment estimate.

Litter size and sex ratio.—We examined 139 young in 74 litters from 47 different females (53 litters and 32 females in Sarek; 21 litters and 15 females in Troms) from mid-May to early June. Mean litter size during this period was 1.88 young (95% *CI* = 1.68–2.07) and ranged from 1 to 4 young. Sex was determined for 128 young. Of these, 77 (60%) were females and 51 (40%) were males (57% and 68% females in Sarek and Troms, respectively). This differed from an expected 1:1 ratio ($\chi^2 = 5.28$, *d.f.* = 1, $P = 0.02$). No significant difference was found in the sex ratio among young between Sarek and Troms ($\chi^2 = 1.54$, *d.f.* = 1, $P = 0.2$).

Discussion

We detected no reproduction among 2-year-old females ($n = 11$) although some could have reproduced at 2 years of age but lost their young before denning was detected. Wolverine females seem to produce young no earlier than 3 years of age, and average age of 1st reproduction among 6 females monitored to 1st reproduction was 3.4 years. The late onset of reproduction in female wolverines has management implications, because the proportion of reproducing females in younger age classes affects population growth, and hence population viability and sustainable harvest rates (e.g., Pimm et al. 1988).

Wolverine reproduction was low in our study. Mean proportion of females (3 years old) reproducing each year was 0.53 (annual $\bar{X} = 0.58$), and mean annual birth rate was 0.74 young per female. This is in the upper range of earlier studies reporting proportion of females reproducing each year of 0.38–0.57 and birth rates of 0.43–0.89 (Copeland 1996; Krebs and Lewis 1999; Lofroth 2001; Magoun 1985). Importantly, these reproductive rates and the late onset of reproduction places the wolverine at the lower end of productivity compared to other large carnivores (e.g., Andrén et al. 2002; Fritts and Mech 1981; Weaver et al. 1996). Thus, wolverines may have a low resilience to population disturbance and a low capacity for demographic compensation for high mortality.

Results from this 1st large-scale field study of wolverine reproduction confirm that studies of reproductive tracts may overestimate wolverine productivity. This indicates that young are lost during pregnancy, early after parturition, or both. Losses probably do not occur before implantation, because a unique feature of delayed implantation in mustelids is that there is minimal intrauterine death of embryos during the prolonged preimplantation period (Mead et al. 1993), and the number of corpora lutea approximates the number of unimplanted blastocysts (e.g., Liskop et al. 1981; Rausch and Pearson 1972). However, pregnancy failure at implantation might occur (Arthur and Krohn 1991).

Mean litter size (1.88) of wolverines in our study area were in the range of mean litter sizes from other studies (1.8–2.0—Copeland 1996; Krebs and Lewis 1999; Magoun 1985), but smaller than sizes of litters excavated from dens in March–May (2.4–2.5—Myrberget and Sørumgård 1979; Pulliainen 1968). In utero litter sizes were even larger (2.6–3.5—Banci and Harestad 1988; Liskop et al. 1981; Rausch and Pearson 1972). Similarly, Frost et al. (1999) concluded that corpora lutea, blastocysts, and placental scars are likely to overestimate litter size at birth in fishers (*Martes pennanti*).

There was a bias toward females among young. In a species such as the wolverine with a multimale mating system (Ferguson and Larivière 2004), a deficit of males, if not too large, should not negatively affect population growth rate. Conversely, it could lead to higher population growth rate in nonmonogamous species (Caughley 1977; Solberg et al. 2002). Although survival of young is higher for males than for females (Persson et al. 2003), the recruitment estimate still showed a slight female bias among juveniles entering the subadult age class. However, we think the biased sex ratio at weaning has little effect on the growth of this population.

Our findings that female wolverines have a low birth rate and delayed onset of 1st reproduction (3 years) have demographic consequences. Wolverines are ecologically similar to other large carnivores and experience similar conflicts with humans. Management plans often include lethal control as primary means for reducing conflicts. Low reproductive rates result in a low capacity for demographic compensation for increased mortality, especially mortality of adult females (cf. Boyce 1992; Stearns 1992). Moreover, this affects the vulnerability of populations, because populations with low reproductive rates are generally more vulnerable than populations with high reproductive rates (Pimm et al. 1988; Ruggiero et al. 1994). Such demographic considerations, accentuated by low population densities, suggest that wolverines should be managed over large areas and within these areas human-induced mortality should be kept low. Therefore, it is necessary for wildlife managers to consider wolverine demographics when

Table 1.—Summary of annual reproduction for female wolverines (3 years old) in Sarek, northern Sweden, and Troms, northern Norway. The 1st year of monitoring is excluded for females captured in connection with denning (numbers within parentheses are not included in summary statistics).

Year	Number of females[a]	Reproduction[b]	Proportion of females that reproduced	Number of young	Annual birth rate[c]
1994	(2)	(0)	(0.00)	(0)	(0.00)
1995	(1)	(1)	(1.00)	(2)	(2.00)
1996	(8)	(1)	(0.12)	(1)	(0.12)
1997	13	6	0.46	15	1.15
1998	11	9	0.82	7	0.64
1999	14	4	0.29	1	0.07
2000	14	6	0.43	9	0.64
2001	11	8	0.73	10	0.91
2002	20	15	0.75	20	1.00
Total	83	48	0.58 ± 0.21	62	0.74 ± 0.38

[a] Number of females (3 years old) monitored.
[b] Number of females (3 years old) reproducing, based on denning behavior.
[c] Number of young in May–June divided by number of females (3 years old) monitored.

developing and implementing conservation policies and harvest regulations.

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