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Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia

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Minimum numbers of wolverines *Gulo gulo* were estimated for Scandinavia, based on the average number of active dens recorded in 1995-1997. To estimate the proportion of females active at dens, we followed individual females using radio-telemetry in northern Sweden, northern Norway and south-central Norway. The sex and age structure of the population was estimated based on a sample of wolverines harvested before the introduction of protective measures and harvest restrictions. Our results are compared with those found in other published wolverine studies, mostly from North America. The Scandinavian population of one-year-old and older wolverines was estimated at 413 ± 71 (SD) individuals (265 ± 55 in Sweden and 147 ± 25 in Norway). This method gave a lower population estimate than those found in earlier surveys based on summation of local (municipality) estimates (Troms) and on local tracking surveys (Nordland). The differences may be explained by the existence of a large number of undiscovered natal dens in the two counties mentioned above, but the previous estimates were based on methodologies with sources of error that could inflate estimates. The population size in south-central Norway (the Snøhetta plateau, Trollheimen, Reinheimen and Rondane), based on the average number of active natal dens during 1995-1997, was estimated to be 26 ± 7 individuals. This was in concordance with the 23-30 individuals estimated from intensive tracking and radio-telemetry in spring 1995. Monitoring wolverine reproduction as a basis for population estimates could provide an important management tool. Based on our results, we recommend that the management authorities in Norway closely monitor the presently high harvest rate of wolverines in parts of the country, and establish population monitoring methods that allow continuous evaluation of management strategies.

Key words: distribution, Gulo gulo, population estimation, population size, wolverine

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The ecological role of carnivores as important species for the integrity and health of ecosystems is being increasingly recognised (Eisenberg 1989, Kucera & Zielinski 1995). Recently, wolverine *Gulo gulo* populations seem to have increased in density and distribution throughout Fennoscandia following their protection in 1968 in Sweden, 1973 and 1982 in southern and northern Norway, respectively, and 1979 in Finland (Bevanger 1992, Landa & Skogland 1995, Ministry of Agriculture and Forestry 1997). Therefore, wolverines have become increasingly involved in conflicts with man because of their predation on semi-domesticated reindeer *Rangifer tarandus* throughout the year in Fennoscandia, and on free-ranging domestic sheep *Ovis aries* in the summer in Norway (Bjärvall, Franzén, Nordqvist & Åhman 1990, Landa & Tømmerås 1996, Aanes, Swenson & Linnell 1996, Ministry of Agriculture and Forestry 1997). For this reason, limits to population size and distribution, based on social acceptance of their predation, have been advocated as management tools. Permits to kill wolverines due to predation on sheep or semi-domesticated reindeer have been granted in recent years in several areas. These management measures were based on the general evaluation that the wolverine populations were viable. However, the accuracy of the population estimates is uncertain because of the variety of survey methods used for different subpopulations (Bergström, Bø, Franzén, Henriksen, Nieminen, Overrein & Stensli 1993).

The wolverine is mostly nocturnal and occurs in remote boreal mountainous areas. Reported densities range between 0.12 and 2.5 wolverines per 100 km^2 (Banci 1994). Its fragmented distribution and inconspicuous way of living complicate both management and research. Surveys and tracking of wolverines are usually carried out in spring on fresh snow, when the cubs are still inside the natal den (Haglund 1966, Myrberget 1968, Pulliainen 1968, Landa & Skogland 1989). These surveys record wolverines that are one year old or older.

A long-term management policy for wolverines, especially when they are harvested, requires reliable data on population dynamics and population estimates based on a quantitative and repeatable estimation technique. Our objective was to develop a standardised model to calculate the number of one-year-old and older wolverines based on the number of recorded active natal dens. Wolverine natal dens are often temporary constructions in snow drifts, and they may be used repeatedly (Magoun 1985, Lee & Niptanatiak 1996, Landa, Strand, Linnell & Skogland 1998). The dens are found in a variety of habitats, often in steep rocky valleys at the treeline (Landa et al. 1998). If the distribution of wolverine males is determined by females, as suggested for solitary carnivores (Sandell 1989), it seems reasonable to assume that wolverine populations are structured around breeding females. The number and distribution of natal dens could thus have potential for providing an index of wolverine population density (Lee & Niptanatiak 1996) and distribution. To estimate the Scandinavian population, we used the average number of active natal dens recorded from 1995 to 1997. We tested this technique on a small, intensively studied population in south-central Norway, by comparing the results with a population estimate obtained using intensive tracking on snow and radiotelemetry.

Material and methods

Systematic recordings of denning females have been carried out in Sweden since 1974 (Bjärvall & Lindström 1991), and in the three northernmost counties of Norway (Nordland, Troms and Finnmark) since 1991 (Bergström et al. 1993). In the Snøhetta area in south-central Norway, records of wolverine numbers and breeding attempts have been available since the wolverine population was re-established in 1979 (Landa, Strand, Swenson & Skogland 1997).

Since 1991, wolverine reproduction in northern Fennoscandia has been surveyed and recorded using a standardised methodology (Bergström, Bø, Franzén, Henriksen, Nieminen, Overrein & Stensli 1994), based on earlier surveys in Sweden and the Snøhetta area. Once a den locality has been found, it is surveyed in subsequent years and the certainty of successful reproduction is determined on a subjective scale (0 - 100%). The subjective scale was based on criteria of wolverine activity and behaviour as indicators of reproduction. The criteria for 50% certainty are that an assumed adult female (>2 year) visits the site during February - May (observed each time on a minimum of five checks), and that her behaviour suggests that she gave birth (tracks in and out, extensive scent marking, food stores). Reproduction is classified as 100% certain when cubs or cub tracks are seen, if dead cubs are found, or if a lactating female is caught (Bergström et al. 1994). Because our aim was to obtain a reliable figure of the number of reproducing females, we only included records that were at least 50% certain.

To be able to estimate a minimum population size from the number of breeding females, sex ratio, age structure, and the proportion of breeding females should be known. This is obviously a problem, because these parameters may vary with locality and year. However, because we were interested in Scandinavia-wide estimates, we were willing to accept average values representative for Scandinavia.

Female breeding frequency

The proportion of adult females at natal dens was calculated from three radio-telemetry studies carried out in south-central Norway (1990-1995), northern Sweden (1993-1997) and northern Norway (1996-1997). In Scandinavia, 17 radio-marked adult females gave birth 21 times during 37 female-years in northern Sweden (Lindén, Segerström & Stuge 1996). On the Snøhetta plateau in south-central Norway, Landa et al. (1998) reported three breedings by three adult females followed for five female-years. In Troms, northern Norway, seven females gave birth during 10 female-years (A. Landa, R. Andersen & I. Halgundseth, unpubl. data). There was no difference in the breeding frequency among the three study areas; the data were actually slightly underdispersed. This is as expected if the autocorrelation between successive breeding attempts is negative. The breeding frequency is therefore best estimated from the sum of the number of breedings (31) of the total number of female years (52), assuming that the number of breedings is binomially distributed in each area, giving the estimate $\hat{q} = 31/52 = 0.596$.

Number of females

The total number of recorded active dens from 1995 to 1997 are given in Table 1. Assuming that q and the number of adult females $N_j^{(f)}$ in subpopulation j remains approximately constant during these three years, the number of recorded active dens $X_{t,j}$ in subpopulation j in different years t, are random variables identically distributed with the expectation

$$E(X_{t,j}|q) = N_j^{(f)}q \qquad (1).$$

For simplicity, we also assume that the number of breedings in successive years is independent, which is conservative, because breeding in one year is likely to be followed by a year without breeding, thus causing negative covariance between successive $X_{t,j}$'s and less variance in the sum (see e.g. McCullagh & Nelder 1989).

The unknown number of adult females can be estimated using the unbiased estimator

$$\hat{N}_j^{(f)} = \frac{1}{3}\sum_{t=1995}^{1997} X_{t,j} | \hat{q} \qquad (2),$$

the average number of active natal dens within a county or area during 1995 to 1997, divided by the breeding frequency.

Table 1. Number of wolverine dens recorded during 1995-1997 in five Norwegian and four Swedish counties/areas within two classes of certainty, i.e. 50-90 and 100%.

Year	1995			1996			1997		
County/area	50-90%	100%	Total	50-90%	100%	Total	50-90%	100%	Total
Finnmark, N	6	6	12	0	5	5	5	3	8
Troms, N	3	8	11	2	9	11	2	4	6
Nordland, N	1	7	8	0	10	10	4	2	6
Nord-Trøndelag, N	0	0	0	0	0	0	0	1	1
South-central Norway	0	8	8	0	5	5	2	2	4
Nordbotten, S	7	23	30	18	31	49	16	32	48
Västerbotten, S	4	0	4	0	15	15	8	9	17
Jämtland, S	0	1	1	0	1	1	0	4	4
Dalarna, S	0	0	0	1	0	1	0	0	0
Total	21	53	74	21	76	97	37	57	94

Proportion of adults

To estimate the size of the whole population, we also need to know the present proportion of adults in the population. The estimation of this proportion is based on historical hunting statistics consisting of time series of the number of adults $V_{t,j}$ (age >2 years) in relation to the total number $W_{t,j}$ of adults and subadults (age = 1-2 years) caught in different years t and regions j from 1910 until introduction of protective measures and hunting restrictions in Scandinavia about 1970. Because of the large annual variation in cub production, we ignored cubs produced each year. It is reasonable to assume that the number of adults caught in any particular year t and region is binomially distributed

$$V_{t,j} | p_{t,j} \sim \text{bin}(p_{t,j}, W_{t,j}) \quad (3),$$

given the unknown proportion of adults $p_{t,j}$ in that population at that time. It is clear, however, that the proportion of adults may vary considerably among years and regions. Here we assume that the $p_{t,j}$'s are independently beta distributed with unknown expectation μ and variance σ^2. The assumption of independence means that we are ignoring temporal and spatial autocorrelations in the underlying proportion, in the hope that the extra variance in the estimated parameters caused by these dependencies would be small if incorporated in the analysis. With these assumptions, the unconditional distribution of each $V_{t,j}$ is beta-binomially distributed with parameters μ and σ^2 (Anderson 1988). These two parameters can be estimated by maximum likelihood using standard numerical methods.

We assume that the population dynamics determining the distribution of the proportion of adults until protection is representative also for the present population, so that the $p_{t*,j}$'s follow the same distribution as the historical data, that is, the $p_{t*,j}$'s, given μ and σ^2, are independent beta-distributed variables.

Bootstrapping procedure

Relying on an equal sex ratio (see Results), the total size in subpopulation j can be predicted by

$$\hat{N}_j = 2\, \hat{N}_j^{(f)} | p_{t*,j} \quad (4),$$

where $\hat{N}_j^{(f)}$ is given by equation (2) and $p_{t*,j}$ is beta-distributed with expectation $\hat{\mu}$ and $\hat{\sigma}^2$. The uncertainty in the final estimates for the subpopulation j = 1,2,...,n can be found by simulating bootstrap hunting data parametrically (see e.g. Efron & Tibshirani 1993) from the fitted beta-binomial model, and refitting this model for each bootstrap data set to obtain bootstrap estimates $\hat{\mu}^*$ and $\hat{\sigma}^{2*}$. We then simulate one bootstrap value $\hat{q}^*$ for the estimate of the breeding frequency under the assumption that the number of breedings are binomially distributed. Then for each subpopulation j, we simulate the present proportion of adults $p^*_{t*,j} \sim \text{beta}(\hat{\mu}^*, \hat{\sigma}^{2*})$, and simulate den activity data non-parametrically by resampling with replacement (Efron & Tibshirani 1993) from the observed den activity data within each subpopulation to obtain bootstrap estimates $\hat{N}_j^{(f)*}$ of the number of adult females. Substituting these values into equation (4) for each subpopulation j and repeating the procedure say, 500 times, we obtain bootstrap replicates $\hat{N}_j^*$ of all subpopulation sizes. Bootstrap estimates of population size in larger sets S of subpopulations, for example Norway or Sweden, are then given by $\hat{N}^* = \sum_{j \in S} \hat{N}^*_j$. Approximate confidence intervals are then given by, for example, the 0.025 and 0.975 quantiles of the resulting distributions.

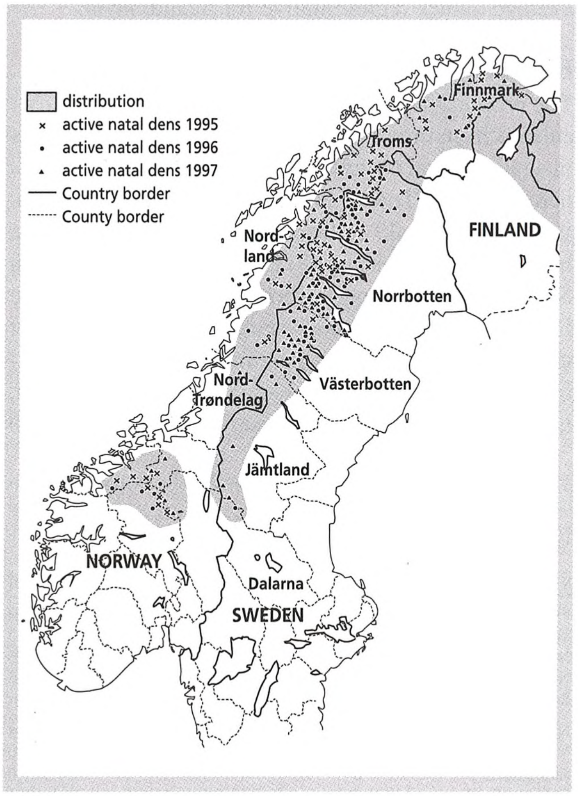

Figure 1. Wolverine distribution and active natal dens in Norway and Sweden during 1995 - 1997.

Table 2. Sex and age distribution of wolverines killed in Scandinavia within 10-year periods from 1910 until protection. Protection was introduced in 1969 in Sweden, and in 1973 and 1982 in southern and northern Norway, respectively.

10-year period	Cubs	Subadults	Adults	% Adults of adults + subadults	Sex ratio Males/females
1910	7	3	8	72.7	1.3:1
1920	3	3	5	66.7	0.7:1
1930	6	3	5	62.5	0.4:1
1940	11	12	18	60.0	1.2:1
1950	46	22	44	66.7	1.0:1
1960	86	33	100	75.2	1.2:1
1970	28	12	33	73.3	1.1:1
1980	4	1	3	75.0	0.6:1
Total	191	89	216		N = 245:223[1)]

1) Sex designations were lacking for some specimens which were age determined.

Results

In 1995-1997, an average of 85 active dens were documented in Scandinavia. An average of 62 was verified at 100% certainty; the rest had 50-90% certainty (Fig. 1). In Sweden, the number of natal dens increased from 35 in 1995 to 66 in 1996 and 69 in 1997. In Norway, 39 dens were recorded in 1995, compared to 31 in 1996 and 25 in 1997. However, as the number varied from area to area during these three years, south-central Norway and the county of Finnmark had higher numbers in 1995 (see Table 1).

Sex ratio

Natural carnivore populations are usually assumed to have equal sex ratios. For this study, we assumed a 1:1 sex ratio. Males comprised 52% of the wolverines killed in Scandinavia between 1910 and protection (Table 2), which was different neither from the expected sex ratio ($\chi^2 = 1.03$, df = 1, $P > 0.05$), nor from the total sample (1846-1992; Landa & Skogland 1995). No difference in the sex ratio was found among the three regions in Scandinavia (Landa & Skogland 1995). Live-captured wolverines, caught in box-traps in Scandinavia and North America, have a sex ratio of approximately 1:1; data from 83 live-captured wolverines gave a sex ratio of 41:42 ≅ 1:1 (Table 3).

Estimated numbers and a test of the model

When fitted to the hunting statistics data, the beta-binomial model gave an estimate of the proportion of adults equal to $\hat{\mu} = 0.72$, with a standard error (found by bootstrapping) equal to 0.028. The estimate of the natural variability in $p_{t,j}$ was equal to $\hat{\sigma} = 0.076$. Estimates of minimum wolverine population sizes based on these formulas were 265 ± 55 (SD) in Sweden, 147 ± 25 in Norway, and 413 ± 71 in Scandinavia as a whole. Estimates of total subpopulation sizes with confidence intervals calculated following the procedure described in the previous section are given in Table 4. In 1995, a tracking survey combined with radio-telemetry carried out in the south-central Norwegian wolverine population (Snøhetta and surrounding mountains) resulted in an estimate of an absolute minimum of 23 and an assumed minimum of 30 individuals. The average number of active dens (5.6) recorded during 1995-1997 in this population gave an estimate of 26 ± 7 individuals.

Table 3. Sex and age structure of live-captured wolverines in Scandinavia and North America. Cubs were 0-1 year old (dependent cubs, i.e. <6 months old, were excluded in reports from North America, except in Magoun 1985). Capture methods are classified as box traps, secondary dens where females and cubs were captured, and helicopter where animals were darted from the helicopter.

Location	Capture method	Sex ratio males/females	N	% Cubs	% Subadults	% Adults	N	% Adults of adults + subadults	Source
Scandinavia									
SC Norway	Box traps	1.4:1	7:5	8	23	61	12[1]	73	Landa et al. 1998
N Norway	Sec. dens	0.41:1[2]	7:17	71	0	29	24	-	A. Landa et al. unpubl. data
N Sweden	Sec. dens	0.64:1[2]	23:36	56	3	41	59	-	Lindén et al. 1996
North America									
SW Yukon	Box traps	1.0:1	5:5	20	7	73	15[3]	92	Banci 1987
NW Alaska	Box traps	0.85:1	12:14[4]	33	17	54	22	81	Magoun 1985
NW Montana	Box traps	0.9:1	11:13	0	29[5]	71	24	71	Hornocker & Hash 1981
NC Idaho	Box traps	1.2:1	6:5	0	27	73	11	73	Copeland, Cesar, Peek, Harris, Long & Hunter 1995
N Yukon	Helicopter	2.5:1[2]	10:4	7	7	86	14	-	D. Cooly (in Banci 1994)
SC Alaska	Helicopter	2.4:1[2]	12:5	-	24	7	17	-	Whitman & Ballard 1984

1 Includes two unmarked adult females.
2 Biased due to capture methods and therefore not used in comparison.
3 Includes five unmarked animals.
4 Sex ratio includes two wolverines of unknown age.
5 Sub-adults and cubs-of-the-year were not separated.

Table 4. Minimum population estimates of wolverines by county and region in Scandinavia, based on average number of recorded active dens during 1995-1997.

County	$\hat{N}_j$	SD	95% confidence interval		90% confidence interval		80% confidence interval	
Finnmark, N	38.7	10.1	22	60.5	23.7	56.6	26.6	51.4
Troms, N	43.4	11.2	27.5	70.4	29.2	63.3	31.6	57.4
Nordland, N	37.2	8.8	25.4	56.6	26.6	51.9	29.5	48.1
Nord-Trøndelag	1.5	1.3	0	4.6	0	4.1	0	3.5
South-central Norway	26.3	7.3	16.6	45.6	17.8	40.1	19.4	36.2
Norway	147.4	25.1	108.6	202.75	112.8	192.3	121.3	185.6
Nordbotten, S	197	44.7	132.9	296.2	140.6	271.8	149.3	254.4
Västerbotten, S	57.4	21	23	103.1	31.2	95.4	35.2	83.6
Jämtland, S	9.3	4.4	3.7	18.6	3.9	16.9	4.2	15.5
Dalarna, S	1.5	1.3	0	4.6	0	3.8	0	3.3
Sweden	265.3	54.7	191.6	385.5	198.1	352.7	212.6	338.9
Scandinavia	412.6	70.6	309.6	567.8	324.5	540.6	339.6	507.1

Discussion

Recorded numbers of dens and problems

During periods when nutritional conditions are good, most females in an area will probably have a den and will therefore be recorded during field work, whereas the same females will not be recorded in a year with poor conditions. The number of active natal dens used in our model therefore was based on average numbers during three years, thus avoiding variations between years.

There are two main sources of error when recording natal dens: 1) classifying dens used by yearling females (Landa 1992), and 2) multiple den use by females. Secondary dens have been observed as far as 13 km from the primary den (M. Lindén, J. Persson & P. Sägerström, unpubl. data). The same female could therefore be counted twice if neighbouring den sites were not carefully examined with this possibility in mind. This fact is especially important because the new compensation scheme in Sweden for semi-domesticated reindeer losses to carnivores makes it economically profitable to verify as many active wolverine dens as possible within the area of reindeer husbandry. Nearly SEK 100,000 (about USD 13,000) was paid to compensate for each active den in 1996 and 1997.

As discussed below, the estimates of population size are conservative, especially in Norway, where the true number may be higher, based on recent experience in Sweden (see below). In addition, both countries have counties with very poor survey coverage (Nord-Trøndelag in Norway and Jämtland in Sweden). More dens probably exist in these parts of the continuous range, but systematic surveys have not been carried out.

The number of recorded, active dens varies from year to year. Some of this variation is undoubtedly due to variation in breeding conditions, but in some cases it may also depend on methodology and the motivation of the personnel involved. The 100% increase in the number of active dens in Sweden, from 35 in 1995 to 66 in 1996 and 69 in 1997, is an example of the latter. A new compensation scheme for losses of domestic reindeer to carnivores was introduced in 1996. Compensation is paid according to the number of carnivore reproductions documented in the grazing areas. So the high compensation paid for reproducing carnivores, may have lead to increased efforts to search for and report active wolverine dens since 1996. Thus, the apparent increase probably simply was the result of increased survey efforts, and should not be interpreted as an increase in the actual number of wolverine dens in Sweden. Because each reported den had to be checked by representatives of the County Administration, the criteria used to verify dens were comparable to those used previously.

Searching for active dens is carried out with different intensity in different areas and is also affected by the topography. Hence, the likelihood that all dens are found varies from one area to another. The fact that the number of recorded active dens in Sweden almost doubled from 1995 to 1996/1997 suggests that the results reported from northern Norway are conservative, owing to a topography which is difficult to monitor, and lower motivation to find and report active dens. Furthermore, the recording of active natal dens was introduced only recently, and still has not been established as a standard monitoring method in every county. Results from south-central Norway are probably more reliable because the wolverine population within this area has been monitored intensively since 1979 (Landa & Tømmerås 1996, Landa et al. 1997).

Far fewer natal dens were found in Troms and Nordland (Norway) than were expected from previous population estimates, which were 80-120 and 70-90, respectively, of a minimum of 200 individuals in all of northern Fennoscandia (Bø & Schølberg 1990, Bergström et al. 1993). This could be due to insufficient searching, but in spite of increased efforts in recent years, the number of active natal dens recorded in Norway has decreased while harvest rates have increased. The previous numbers in Troms were based on a weak data set (Bergström et al. 1993). A very similar methodology led to a highly inflated population estimate for the brown bear *Ursus arctos* in Norway in the 1970s and 1980s (Swenson, Wabakken, Sandegren, Bjärvall, Franzén & Söderberg 1995). The method used in Nordland may be somewhat more reliable (Bø & Schølberg 1990), but the results are more than seven years old. Minimum estimates from both these counties were 1.9 times higher than our estimate, and their assumed minimum estimates were 2.4 and 2.8 times higher. The previous estimate of the entire Fennoscandian wolverine population was approximately 250 individuals, including 20 wolverines in the counties of Nord-Trøndelag, Norway, and Jämtland, Sweden (K. Knutsen, unpubl. data), and the south-central Norwegian wolverine population consisting of about 30 individuals (Landa et al. 1997).

Proportion of females giving birth

The proportion of radio-marked females giving birth in Scandinavia was about 60%, which was used in our model. Our estimate is probably biased because two of the samples (northern Sweden and northern Norway) consisted of selectively captured adult females at secondary dens, thus the proportion of females active at dens will decrease when the females have been followed for some years. The $\hat{q} \cong 60\%$ used in our model is therefore most likely too high, thus resulting in a conservative estimate. Two North American studies reported lower rates; Magoun (1985) reported 40% and the general impression of Hornocker & Hash (1981) was that about 50% of the females in their study area had cubs each year.

The age structure of wolverine females in a given area will influence the number active at dens. Investigations of reproduction in wolverines consistently report that females have their first litter when they are two years old, i.e., they mate first as yearlings. However there is a large variation in the proportion of pregnant yearlings (subadults). Rausch & Pearson (1972), Liskop, Sadleir & Saunders (1981), and Banci & Harestad (1988) reported proportions to be 50%, 85%, and 7%, respectively in North America. Uncertain age determination methods in the first two studies may account for some of the variation (Banci & Harestad 1988, Landa 1992, Banci 1994). Furthermore, the litter sizes of wolverines increase with female age, whereas litter frequency decreases with age (Banci & Harestad 1988).

Surveys of wolverine carcasses have shown that between 59% and 92% of adult females are pregnant each year. The proportion of harvested adult females that were pre or post-partum was 59% in Norway (Myhre 1968, N = 29). North American data were more variable, with higher proportions of harvested adult females that were pre or post-partum; 92% in Alaska and the Yukon (Rausch & Pearson 1972, N = 98), 88% in British Columbia (Liskop et al. 1981, N = 26), 73% in the Yukon (Banci & Harestad 1988, N = 79). These proportions are generally higher than those found in the live-capturing studies referred to above.

Although most adult females may mate every year, not all give birth (Magoun 1985). The main issue for our estimator model is whether or not all pregnant females are active at a den site. Banci & Harestad (1988) believed that cubs were probably lost early in pregnancy, but field data from excavated dens have shown that cubs also may die in the den (Landa et al. 1997). The condition of the female before implantation in December-February may also be a factor determining whether or not cubs will be born (Banci 1994). Analyses of reproduction from harvested animals may overestimate the number of reproductively active females at natal dens. It is likely that some of the females regarded as pre or post-partum, based on placental scars or foetuses, reabsorbed their embryos due to poor nutritional condition (Banci & Harestad 1988), and thus would not have been active at a natal den. The lower proportion of females active at dens found by telemetry than indicated in analyses of reproduction in harvested animals supports this.

Sex ratio and age distribution

The sex ratio, based on killed wolverines in Scandinavia was not different from the expected 50/50 distribution. However, sex ratios of killed wolverines in North America were skewed toward males ($\chi^2 = 24$, df = 1, P < 0.001, Rausch & Pearson (1972) and χ^2 = 5.34, df = 1, P = 0.02, Banci (1987)). Banci (1994) believed that wolverines captured in live traps reflected the true age and sex distribution of wolverines in a given locality. In studies where the sex ratio was in favour of males (north Yukon and south-central Alaska), the wolverines were caught after immobilisation with a dart gun from a helicopter. The capturing was often carried out during the denning period of the females, which might explain the skewed sex ratio towards males (Banci 1994). In northern Sweden and northern Norway excavation of secondary dens has mainly been used to catch wolverines, thus biasing the sample towards females (see Table 3).

The hunting statistics from 1910 until protection show that adults comprised about 72% which we used in our model. In North America, Banci (1987) found 73% adults using a similar age classification method, and Rausch & Pearson (1972) found 68% with a classification method that was nearly the same. The proportion of adults found among live-captured animals in Scandinavia (excluding animals caught using selective methods of catching) was 73%, but the sample size was too small to be used in our study. However, this proportion averaged 78% ± 0.09 (SE, range 71 - 92%) in five live-capturing studies (south-central Norway and North America, see Table 3). The variation in the age structure of killed wolverines in Scandinavia, when divided by area and period, suggested that restrictions on time, methods, and area of harvest might have resulted in a selective sample (Landa & Skogland 1995). However, data from animals killed before protective restrictions were implemented are less selective and based on a larger sample size than data obtained from live-trapping. The age distribution based on data from harvested animals in Scandinavia did not differ much from North American data.

Management implications

Estimates of the distribution and population density of the wolverine are obtained using numerous methods throughout its range, although all are based on the finding of tracks on snow (e.g. Becker 1991, Bjärvall & Lindström 1991, Novikov 1994, Zielinski & Kucera 1995, Ministry of Agriculture and Forestry 1997). The methodology presented in this paper, using counts of natal dens as a basis for population estimation, might be an additional useful tool. A population estimate made with our method conformed well to an estimate based on a tracking survey carried out during the same year (1995) in the well-studied south-central Norwegian wolverine population. More knowledge about the actual proportion of females active at natal dens and the age and sex structure within populations is needed to improve the method in the future. However, the method as used is conservative and thus applicable when issuing control permits, provided that field records of females active at natal dens are carried out in a reliable way. Furthermore, this method may be adapted, in the future, to helicopter-based surveys, to allow censuses in large and remote areas. However, the method used to estimate the numbers of wolverines should always depend on the purpose, the topography, available resources, the size of the area which needs to be covered, and the degree of accuracy required.

The practice of killing wolverines to reduce damage to livestock and domestic reindeer is widely applied in Norway; 56 were killed legally during 1993-1998. The Swedish management authorities issued permits for the destruction of three active dens (i.e. killing of female and cubs) in 1997, the first legal removal of denning females and cubs since 1986. In addition, illegal hunting has been documented in both Norway and Sweden. Some of the recent management actions in Norway should be re-evaluated in view of the data reported here. For example, permits were issued to kill 10 wolverines in Troms during 1996-1997. These constituted almost a quarter of the estimated population (43 ± 11), based on wolverine dens found during 1995 - 1997. This is definitely a high harvest rate, unless the goal is to reduce the population. The four permits issued in Nordland in 1996 appeared more reasonable, based on our population estimate (37 ± 9). Even though our population estimates are likely to be conservative, the present data do not support the high quota in Troms.

Even though wolverine populations are considered to have a relatively low resilience (Weaver, Paquet & Ruggiero 1996, Landa & Skogland 1995, Landa et al. 1998), populations began to increase and recolonise parts of their former range following protection (Landa & Skogland 1995). Nevertheless, it seems that in many places wolverine population densities remain much lower than before the turn of the century (Bjärvall & Lindström 1991, Landa & Skogland 1995), and the wolverine has not yet reoccupied all of its former range, especially in southern Scandinavia (Landa 1997). The social dynamics of wolverines is poorly known, and removal of a few individuals may have unexpectedly large consequences in small populations of carnivores. For example, it has been suggested that the killing of adult male brown bears led to increased mortality among cubs (Swenson, Sandegren, Söderberg, Bjärvall, Franzén & Wabakken 1997).

In conclusion, we recommend that the search for and verification of natal dens be given higher priority throughout the distribution area of the wolverine. This is especially important in Troms, Nordland and Nord-Trøndelag, in Norway, and Jämtland, in Sweden. Monitoring of den sites and mapping of dens using the stringent criteria that have been developed (Bergström et al. 1994) should continue on an annual basis throughout the range of the species in Fennoscandia. If harvest quotas are based on population estimates using the method reported here, unintentional overharvesting can be avoided and management authorities would have an obvious incentive to find and document natal den sites as completely as possible. We recommend a re-evaluation of our proposed census method, using data on the sex ratio, age structure and proportion of adult females that breed, from the ongoing wolverine research projects in Sweden and Norway when sufficient data become available.

Survival of cubs varies among years and areas (Landa et al. 1997). In areas where harvest is planned, the number of surviving cubs should also be monitored, as they represent the 'surplus' which can be harvested after accounting for natural mortality. It is especially important to monitor the number of cubs produced in areas with small population numbers (e.g. the southern Norwegian core conservation area).

In 1996, the wolverine was reclassified from 'vulnerable' to 'rare' in the Norwegian National Red Data List. In Sweden, the wolverine is listed as 'vulnerable', even though there seem to be many more wolverines in a smaller area than in Norway. The species is listed as endangered in Finland, where the authorities estimate that there are at least 110 wolverines (Ministry of Agriculture and Forestry 1997). Based on the most recent IUCN criteria (IUCN 1996), we conclude that the Fennoscandian wolverine population as a whole should be classified as vulnerable.

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