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Authors: Landa, Arild, and Skogland, Terje

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# The relationship between population density and body size of wolverines *Gulo gulo* in Scandinavia

Arild Landa & Terje Skogland†

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The number of wolverines *Gulo gulo* in Scandinavia has declined dramatically since the middle of the last century, and the numbers killed continued to decrease until the species was protected. In 1968 the species was protected in Sweden; in 1973 the wolverine was given full protection in southern Norway and protection during the breeding period in northern Norway; and in 1982 the species was also given full protection in northern Norway. The protection has resulted in some increase in number, but the population density remains much lower than at the turn of the century, and the wolverine has yet not reoccupied all of its former range. Our analyses show that body size, as reflected by skull characters, was inversely correlated with population density from the mid-nineteenth to the mid-to late twentieth century. In contrast we found a strong decline in body size in the decades after ca 1960. The unexpectedly low wolverine resilience in this century may be explained by an energy-restricted model whose main factors include: 1) habitat fragmentation, 2) loss of habitat, 3) extinction of the dominant predator, the wolf *Canis lupus*, and 4) a maximised turnover in managed ungulate populations that has resulted in less natural mortality and fewer weakened animals available for scavengers and less efficient predators like the wolverine.

Arild Landa & Terje Skogland†, Norwegian Institute for Nature Research, Tungasletta 2, 7005 Trondheim, Norway

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The wolverine *Gulo gulo* is the largest terrestrial mustelid. It has a circumpolar distribution in the tundra and taiga (Makridin 1964, Kvam et al. 1988) and is one of four large carnivores found in Scandinavia; the other three being the brown bear *Ursus arctos*, the wolf *Canis lupus*, and the lynx *Lynx lynx*. Until the beginning of this century, the species was distributed throughout forested and mountainous areas as far south as the southernmost counties of Norway (Johnsen 1928), and Värmland in the southern part of central Sweden (Lönnerberg 1936). Today wolverines are found mainly in mountainous areas in the northern parts of Norway and Sweden (Kvam et al. 1988). Wolverine distribution in the Palearctic is sympatric with that of both wild and domestic reindeer *Rangifer tarandus*, which constitutes the most important winter food source for wolverines (Pulliainen 1968, 1988, Myhre & Myrberget 1975, Semenov-Tyan-Sjanskii 1982).

Because of their predation on domestic animals, the large carnivores have traditionally been regarded as pests. The statistics on bounties paid by the state, since 1827 in Sweden and since 1845 in Norway, show a dramatic decrease in the number of wolverines killed over more than a century, until the enactment of protective legislation (Fig. 1). Because the predation conflicted with sheep and reindeer herding and because of the official policy of rewarding the killing of wolverines, it is reasonable to believe that hunting statistics reflect population size until protection. However, hunting statistics after about 1970 are not a reliable indication of population size due to a series of management regulations. The species was totally protected in Sweden in 1968. In southern Norway (Jotunheimen) the last remaining population was exterminated by the killing of seven wolverines in 1967 (Landa unpubl. data). In 1973, when the species was protected in south-

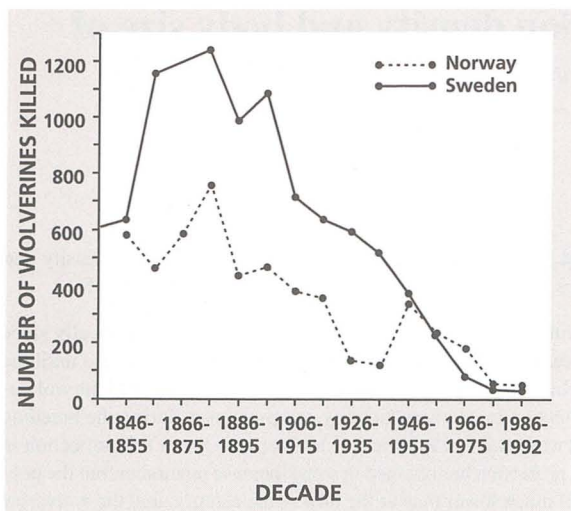


Figure 1. Hunting statistics on wolverines per decade during 1836-1992. The wolverine was totally protected in Sweden in 1968, totally protected in southern Norway and protected during the breeding period in northern Norway in 1973, and finally fully protected throughout Norway in 1982.

ern Norway and in northern Norway during the breeding period, protection was granted because wolverines were scarce and in danger of extinction (Myrberget & Sørungård 1975, Ahlén 1977). With the enactment of the Wildlife Act of 1982, the wolverine became totally protected throughout Norway.

There is good evidence that the population has increased following protection (Heggberget & Myrberget 1980, Ahlén 1981). One area in central southern Norway, the Snøhetta wild reindeer region, had been recolonised by wolverines around 1979 (Kvam 1980). The statistics on compensation paid for wolverine predation on sheep and domestic reindeer in Norway have shown an increase from 1973, when it was first paid, until about 1985 (Kvam et al. 1988). Although this increase in compensation payments may partly reflect the spread of information among farmers and reindeer herdsman about the compensation law, there is little doubt that most of the increase in compensation payments is attributable to many areas being recolonised by wolverines (Kvam et al. 1988, Kvam 1980, Loen 1991). However, the wolverine has not yet been able to recolonise all of its former range. In Norrbotten County, Sweden, the distribution of the denning sites of female wolverine seems to be more widely spaced today than earlier (Björvall & Lindström 1991).

An inverse correlation between body weight and population density has been observed in many mammals (Scheffer 1955) and is usually attributed to food limitation (Klein 1970, 1981, Skogland 1983). At low population density, there are ample food resources per individual and the animals may grow large, whereas in popula-

tions approaching their carrying capacity, resources become scarce and competition for food increases, which may result in decreasing body weights at the highest densities. This has been documented for several cervids (Serveringhaus 1955, Julander et al. 1961, Klein 1967, Leader-Williams 1988). In Scottish red deer *Cervus elaphus*, there are large differences between sexes in the effect of density on body weight, explained by the greater need for food and protein by males (Clutton-Brock et al. 1982). Skogland (1989) showed increased sexual dimorphism with decreasing food availability in reindeer. This indicates that when food is limited, females allocate more energy than males into reproduction at the expense of their own growth.

Studies involving density-dependence in predators are scarce in the literature. Messier (1987) reported a relationship between moose density and growth and body size of wolves in southwestern Québec. The absence of other ungulate species at moose densities below 0.4 moose/km<sup>2</sup> clearly determined the variation in wolf growth and body size in Messier's (1987) study. However, most predators are polyphagous, which enables them to switch between different food sources when one prey becomes scarce. In addition, most predators produce relatively large litters in comparison to non-predatory species, resulting in greater flexibility in birth rates (Fowler 1987). These qualities enable them to track environmental fluctuations closely. Even so, as Messier's (1987) study indicated, we should expect density-dependence to be expressed in factors such as body size in predators as in other mammals. This suggests that parameters of size in both male and female wolverines should be correlated with population density, which in turn should be correlated with competition for food resources in relation to available habitat.

Our hypothesis is that there should be an inverse relationship between population density and body size of wolverines in Scandinavia. We also explore the question: Why have population density and distribution not returned to their former levels.

## Material and methods

The present study is based on wolverine skulls and other material collected by natural history museums and wildlife research institutions. The material consists of 632 wolverine skulls out of which 234 males and 217 females were collected before legal protection was enacted, and 50 males and 42 females were collected afterwards. The skulls were preserved at the Norwegian Institute for Nature Research, Trondheim, Norway, the Zoological Museum of Bergen, Norway, and the Swedish Museum of Natural History, Stockholm. Due to inaccurate collection procedures and loss of original material, sex determination and/or skulls were lacking for 89 specimens.



## Age determination and skull measurements

The roots of incisors, premolars or canines were extracted from the jawbones, softened in a water bath, and sectioned longitudinally at 10-15 microns. The sections were stained blue with a solution of Haematoxylin, sodium iodide and water. Age was determined by counting annual incremental lines in the cementum (Morris 1972, Grue & Jensen 1979). Four males and two females of known age from zoos were used to confirm the dental age determinations but were not included in the analyses.

Cranial development was classified on a scale of 0-4 after having evaluated the closure of 1) the palatal suture (fissure), 2) the zygomatic arch suture, and 3) and 4) the internasal sutures (Fig. 2). Evaluation of suture closure was used thereafter to verify the dental age determinations of animals estimated to be younger than two years of age. Suture evaluation was used when the two methods gave different results. Date of birth was assumed to be 1 March.

The skulls were measured according to Duerst (1926), i.e. the profile length, condylobasal length and zygomatic breadth were measured (Fig. 3). Many of the skulls preserved were damaged so that not all three measurements could be made.

## Estimation of missing values

The archive files at the three different institutes gave different kinds of body weights; 218 were skinned carcass

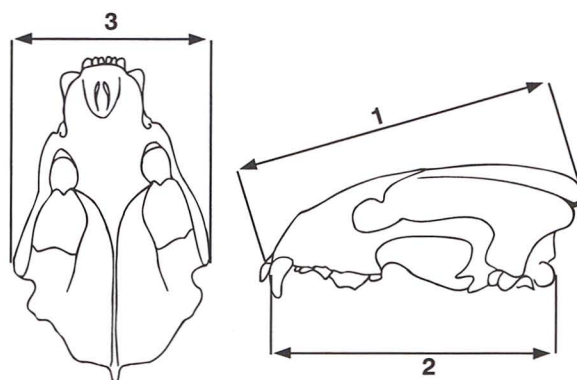


Figure 3. Skull size measurements of wolverine including: profile length (1), condylobasal length (2) and zygomatic breadth (3).

weights, 95 were total weights and 32 were skinned carcass weights without extremities. For 95 specimens, all three values were recorded. A regression analysis on the relationship between skinned carcass weight ( $x$ ) and total weight ( $y$ ) was highly significant in animals younger than nine months ( $r^2 = 0.98$ ,  $F = 171.74$ ,  $P = 0.006$ ) using the equation  $y = 550.3 + 1.14x$ . It was also highly significant for animals older than nine months ( $r^2 = 0.61$ ,  $F = 22.21$ ,  $P < 0.001$ ) using the equation  $y = 5998 + 0.65x$ . The 32 animals with carcass weights without extremities were all older than nine months. The regression equation against total weight was highly significant ( $r^2 = 0.91$ ,  $F = 111.58$ ,  $P < 0.001$ ) with the equation  $y = 2611 + 1.05x$ . All body weight records were transformed into total body weights using the appropriate regressions.

## Statistical Analyses

The wolverine is a rapidly growing animal, and is almost fully grown at nine months of age (Iversen 1972, Wiig 1989). However, some growth occurs during the subadult stage (Wiig 1989, Landa unpubl. data). In order to control for age effects, we used animals older than nine months with age as the covariate in our ANCOVA analyses or the residuals of different size parameters on age as a relative size in our regression models.

Temporal distribution was examined by plotting the sample from each of the areas by year. To evaluate if there were any geographical differences in body size independent of temporal distribution, we conducted an ANCOVA analysis on size measurements from 1955 until protection and after protection in the following three geographical regions: 1) southern Norway (south of Nordland County), 2) Sweden (Jämtland, Västerbotten and Norrbotten Counties), and 3) northern Norway.

We assumed that the hunting statistics of wolverines (see Fig. 1) reflected wolverine densities before protec-

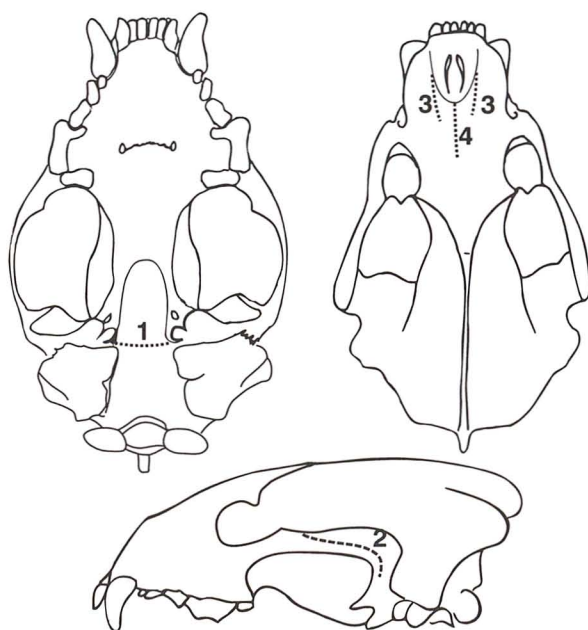


Figure 2. Classification of skull development on a scale including the categories 0-4 based on closure of: all open sutures (0), palatal suture (1), zygomatic arch suture (2), and internasal sutures (3 and 4).

tion. Because bounty statistics were only available per decade, precluding a direct comparison with body size data, we assumed a steady decline in population size until protection. Thus, we modelled the relationship between population density and body size in animals older than nine months by regressing the residuals of size on age against the years from earliest available data until protection was enforced within each of the geographical areas. Records of body weights were scarce before 1960 and totally lacking before 1955, so no analyses were made prior to protection. To evaluate the effects of increased density during protection on size characters, we combined material from a period with low density (from 1955 until protection), with material from a period with higher density (from protection to 1993), and regressed the residuals of size on age against years within each of the areas.

The analyses also included an ANCOVA test of the effects of protection on body size in the different areas, controlling for age in individuals of both sexes older than nine months. To ensure homogenous groups at low density, we selected animals older than nine months in the material from 1955 until protection and tested them against animals older than nine months of the same sex collected after protection was enforced.

Results  
Sex and age distribution

The slight bias towards males (52%) in the total sample (Table 1) was not significantly different from a 1:1 ratio

( $\chi^2 = 0.80$ ,  $df = 1$ ,  $P > 0.05$ ). Furthermore, there were no differences in sex distribution between areas neither before ( $\chi^2 = 1.52$ ,  $df = 2$ ,  $P = 0.466$ ) nor after protection ( $\chi^2 = 0.40$ ,  $df = 2$ ,  $P = 0.817$ ). There was a tendency towards more subadult males and young females before protection ( $\chi^2 = 7.46$ ,  $df = 3$ ,  $P = 0.058$ ), and there were significantly more young males and old females after protection ( $\chi^2 = 8.33$ ,  $df = 3$ ,  $P = 0.039$ , Table 2). Significantly more young males occurred in southern Norway and Sweden after protection than before, but this tendency was less pronounced in northern Norway ( $\chi^2 = 11.05$ ,  $df = 2$ ,  $P = 0.004$ ). Female age structure did not change between areas before and after protection ( $\chi^2 = 3.63$ ,  $df = 2$ ,  $P = 0.163$ ).

Temporal and geographical distribution of the material

The material from before 1900 originated from Sweden; the material from the first half of this century came mainly from northern Norway and Sweden, and only in a few cases did it come from southern Norway (Fig. 4).

The ANCOVA test on size measurements, controlled for age, showed that area explained significant variation in all male size measurements from 1955 until protection, with the largest animals coming from Sweden and the smallest from northern Norway. However, after protection, geographical differences were expressed only in profile length, and the largest males now came from southern Norway (Table 3). In females the effect of area on size measurements was much less expressed. Before

Table 1. Total sample sizes of known sex, age, the three different skull characters, and body weights in wolverines from southern Norway, Sweden and northern Norway from 1845 until protection and from protection until 1994. Animals of known age, including four males and two females from zoos, have not been included in the table.

Character	Sex	Southern Norway		Sweden		Northern Norway		Total
		Before protection	After protection	Before protection	After protection	Before protection	After protection	
Sex	♂	34	10	21	12	179	28	284
	♀	26	8	26	8	165	26	259
Age	♂	34	10	21	12	179	28	284
	♀	26	8	26	8	165	26	259
Profile length	♂	25	7	17	9	139	22	219
	♀	20	4	22	7	114	19	186
Zygomatic breadth	♂	26	6	18	11	142	23	226
	♀	21	5	22	8	118	18	192
Condylobasal length	♂	24	7	16	10	137	21	215
	♀	18	4	22	6	111	19	180
Body weight	♂	22	9	4	12	100	21	168
	♀	12	7	1	6	91	19	136



Table 2. Age and sex distribution before and after protection in wolverines collected in Sweden and Norway during 1845-1993. Animals of known age, including four males and two females from zoos, have not been included in the table.

Sex/Age in years	Before protection						After protection					
	<1	1-2	2-3	3-10	>10	Total	<1	1-2	2-3	3-10	>10	Total
Total sample												
♂♂	89	51	21	68	5	234	23	13	4	10	0	50
♀♀	89	31	33	60	4	217	11	9	2	18	2	42
Total	178	82	54	128	9	451	34	22	6	28	2	92
Southern Norway												
♂♂	12	6	4	12	0	34	3	5	1	1	0	10
♀♀	15	1	5	4	1	26	0	2	1	5	5	8
Total	27	7	9	16	1	60	3	7	2	6	5	18
Sweden												
♂♂	8	7	2	4	0	21	6	3	2	1	0	12
♀♀	10	2	7	7	0	26	1	4	0	3	0	8
Total	18	9	9	11	0	47	7	7	2	4	0	20
Northern Norway												
♂♂	69	38	15	52	5	179	14	5	1	8	0	28
♀♀	64	28	21	49	3	165	10	3	1	10	2	26
Total	133	66	36	101	8	344	24	8	2	18	2	54

protection, profile length tended to be different between areas, but not afterwards. Zygomatic breadth was significantly different between areas, both before and after protection, whereas condylobasal length and body weight were insignificant. The largest females came from southern Norway and the smallest from northern Norway; this did not change with protection. A very low sample size from southern Norway and Sweden may have contributed to the less expressed effect of area in females (Table 3).

Body size during a decline in density and the effect of protection

Relative size measurements from southern Norway from

about 1945 and until protection showed no significant increase with time in any of the size measurements, but were significantly and negatively correlated with male condylobasal length (Table 4). Profile length and zygomatic breadth correlated negatively with year in both males and females between 1955 and 1993. The condylobasal length did not change in males, but decreased significantly in females. Male weight did not change with years, but female weight decreased significantly (Table 5).

Relative size measurements from Sweden from about 1845 until protection showed a significant increase with year in all measurements in both sexes, except in female

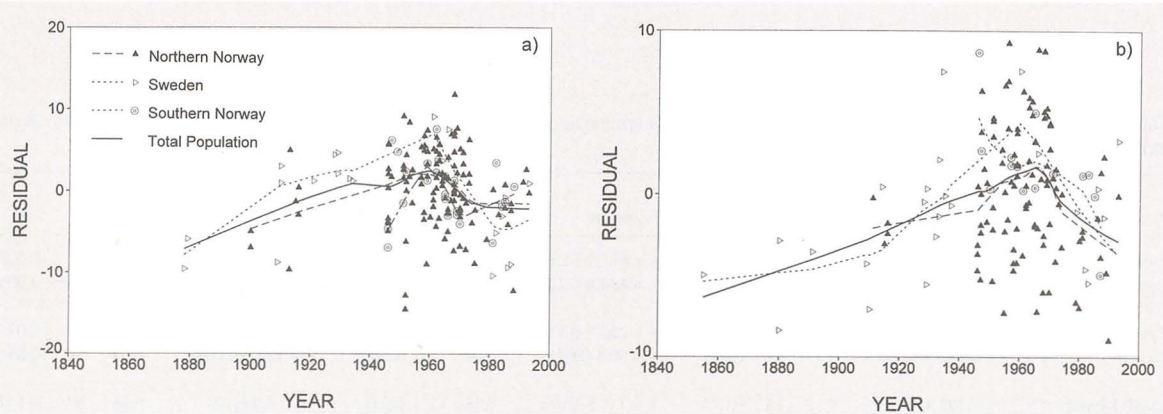


Figure 4. Temporal distribution of relative skull profile length in male (a), and female (b) wolverines older than nine months for northern and southern Norway, Sweden and for the whole population. The lines are illustrating the distribution and are based on a lowess scatterplot smoothing method using an iterative weighted least-squares method fitting 50% of the points using three iterations according to Norušis (1993: 645-655).

Table 3. Effect of geographical distribution on body size measurements in wolverines from 1955 until protection and from protection until 1993, based on an ANCOVA with age as a covariate in all animals older than nine months. The character lengths and breadths are given in mm and body weights in kg. P-value is two-tailed.

Character	Sex	From 1955 until protection								From protection until 1993							
		Southern Norway	N	Sweden	N	Northern Norway	N	F	P	Southern Norway	N	Sweden	N	Northern Norway	N	F	P
Profile length	♂	168.0	14	173.0	4	168.3	70	4.16	0.009	165.4	5	162.0	8	165.0	18	5.08	0.006
	♀	152.3	7	155.1	2	151.5	62	2.58	0.061	149.6	4	148.1	7	147.6	15	1.49	0.246
Zygomatic breadth	♂	106.8	15	107.0	5	106.1	74	7.73	0.000	104.3	4	103.6	10	103.4	18	1.40	0.263
	♀	95.4	7	94.1	2	94.9	63	2.96	0.037	92.5	5	92.4	8	92.3	14	5.97	0.004
Condylobasal length	♂	150.3	14	157.2	3	150.0	75	6.71	0.000	148.7	5	146.7	9	148.7	17	1.16	0.344
	♀	139.1	6	140.1	2	137.7	62	2.12	0.106	137.4	4	137.1	6	135.7	15	1.30	0.302
Body weight	♂	13.7	14	15.2	4	13.8	61	5.04	0.003	13.6	7	13.6	11	13.4	16	1.12	0.356
	♀	11.5	5	10.6	1	11.1	50	1.15	0.336	10.0	7	9.4	6	10.1	15	0.87	0.470

Table 4. Relationship between relative body size (residuals of size on age) and year in declining wolverine populations in the three study areas. P-value is one-tailed.

Residuals	Sex	Southern Norway 1945-1973					Sweden 1845-1968					Northern Norway 1900-1973				
		Equation	r <sup>2</sup>	df	P		Equation	r <sup>2</sup>	df	P		Equation	r <sup>2</sup>	df	P	
Profile length	♂	y = -18.1 + 0.01x	0.00	20	0.464		y = -300.04 + 0.16x	0.67	14	0.000		y = -136.7 + 0.07x	0.51	100	0.012	
	♀	y = 253.7 - 0.13x	0.16	9	0.123		y = -201.3 + 0.10x	0.46	17	0.001		y = -147.0 + 0.08x	0.53	83	0.017	
Zygomatic breadth	♂	y = 86.6 - 0.04x	0.02	21	0.242		y = -142.9 + 0.07x	0.32	15	0.010		y = -53.6 + 0.03x	0.01	104	0.107	
	♀	y = -38.4 + 0.02x	0.01	8	0.424		y = -51.1 + 0.03x	0.10	17	0.095		y = -79.7 + 0.04x	0.03	85	0.067	
Condylobasal length	♂	y = 254.4 - 0.13x	0.14	20	0.049		y = -212.4 + 0.11x	0.64	13	0.000		y = -65.8 + 0.03x	0.03	104	0.046	
	♀	y = 1.4 - 0.00x	0.0	7	0.499		y = -68.1 + 0.03x	0.15	17	0.059		y = -5.2 + 0.00x	0.00	81	0.445	

Table 5. Relationship between relative body size (residuals of size on age) and year in increasing wolverine populations (1955-1995) in the three study areas. P-value is one-tailed.

Residuals	Sex	Southern Norway					Sweden					Northern Norway				
		Equation	r <sup>2</sup>	df	P		Equation	r <sup>2</sup>	df	P		Equation	r <sup>2</sup>	df	P	
Profile length	♂	y = 299.3-0.15x	0.18	18	0.033		y = 817.0-0.41x	0.53	11	0.003		y = 290.3-0.15x	0.09	87	0.003	
	♀	y = 223.2-0.11x	0.32	10	0.036		y = 430.8-0.22x	0.27	8	0.075		y = 251.5-0.13x	0.08	76	0.006	
Zygomatic breadth	♂	y = 308.9-0.16x	0.26	18	0.012		y = 253.5-0.13x	0.18	14	0.059		y = 176.3-0.09x	0.05	91	0.013	
	♀	y = 233.7-0.12x	0.37	11	0.017		y = 60.8-0.03x	0.04	9	0.285		y = 122.9-0.06x	0.04	76	0.051	
Condylobasal length	♂	y = 195.4-0.10x	0.12	18	0.073		y = 718.8-0.36x	0.58	11	0.002		y = 68.4-0.03x	0.01	91	0.157	
	♀	y = 163.4-0.08x	0.32	9	0.045		y = 301.0-0.15x	0.46	7	0.032		y = 118.7-0.06x	0.05	76	0.023	
Body weight	♂	y = -643.6+0.33x	0.00	20	0.445		y = 146980.7-74.1x	0.20	14	0.049		y = 35174.7-17.86x	0.03	76	0.078	
	♀	y = 155901.2-78.9x	0.60	11	0.001		y = 62052.4-31.9x	0.05	6	0.311		y = 85125.5-43.15x	0.17	64	0.000	

zygomatic breadth and condylobasal length (see Table 4). Between 1955 and 1993 all male size measurements decreased significantly with year, except in zygomatic breadth. The only female size measurement that decreased significantly with year was the condylobasal length (see Table 5).

Relative size measurements from northern Norway from 1900 until protection showed a significant increase with year in profile length in both sexes. Neither in males nor in females, did the zygomatic breadth change. Condylobasal length increased with year in males but not in females (see Table 4). Between 1955 and 1993, size measurements decreased significantly with year in male profile length and zygomatic breadth, but did not change in condylobasal length. Body weight did not change with year. All female size measurements decreased significantly with year, except zygomatic breadth (see Table 5).

### Comparing immediately before and after protection

We compared samples collected immediately before protection at low density (from 1955 until protection) with those collected afterwards and at increased densities using an ANCOVA test, controlling for age.

In southern Norway, females showed the most consistent decline in size after protection. Males tended to be smaller in profile length and zygomatic breadth after protection, whereas condylobasal length and body weight did not change. Females declined in all size measurements except in condylobasal length, which only tended to decline (Table 6).

Table 6. Effects of protection on size of wolverines from southern Norway, from 1960 until protection in 1973, and from protection until 1993, based on an ANCOVA with age as a covariate in all animals older than nine months. P-value is one-tailed.

Character	Sex	Size during 1960-1973	N	Size during 1973-1993	N	F	P
Profile length	♂	168.0 mm	14	165.4 mm	5	2.09	0.078
	♀	152.3 mm	7	149.6 mm	4	5.50	0.015
Zygomatic breadth	♂	106.8 mm	15	104.3 mm	4	1.82	0.097
	♀	95.4 mm	7	92.5 mm	5	5.37	0.015
Condylobasal length	♂	150.3 mm	14	148.7 mm	5	0.83	0.227
	♀	139.1 mm	6	137.4 mm	4	2.31	0.085
Body weight	♂	13.7 kg	14	13.6 kg	7	0.08	0.462
	♀	11.5 kg	5	10.0 kg	7	7.05	0.007

Table 7. Effects of protection on size of wolverines from Sweden, from 1955 until protection in 1968, and from protection until 1993, based on an ANCOVA with age as a covariate in all animals older than nine months. P-value is one-tailed.

Character	Sex	Size during 1960-1968	N	Size during 1968-1993	N	F	P
Profile length	♂	173.0 mm	4	162.0 mm	8	15.77	0.001
	♀	155.1 mm	2	148.1 mm	7	3.12	0.059
Zygomatic breadth	♂	107.0 mm	5	103.6 mm	10	4.36	0.016
	♀	94.1 mm	2	92.4 mm	8	2.16	0.093
Condylobasal length	♂	157.2 mm	3	146.7 mm	9	22.06	0.000
	♀	140.1 mm	2	137.5 mm	6	2.43	0.091
Body weight	♂	15.2 kg	4	13.6 kg	11	5.93	0.008
	♀	10.6 kg	1	9.4 kg	6	1.39	0.173

Table 8. Effects of protection on size of wolverines from northern Norway from 1955 until protection in 1973, and from protection until 1993, based on an ANCOVA with age as a covariate in all animals older than nine months. P-value is one-tailed.

Character	Sex	Size during 1960-1973	N	Size during 1973-1993	N	F	P
Profile length	♂	168.3 mm	70	165.1 mm	18	9.28	0.000
	♀	151.5 mm	62	147.6 mm	15	9.07	0.000
Zygomatic breadth	♂	106.1 mm	62	103.4 mm	18	16.20	0.000
	♀	94.9 mm	64	92.3 mm	14	9.92	0.000
Condylobasal length	♂	150.0 mm	75	148.7 mm	17	2.01	0.066
	♀	137.7 mm	62	135.7 mm	15	4.68	0.001
Body weight	♂	13.8 kg	61	13.4 kg	16	3.11	0.016
	♀	11.1 kg	50	10.1 kg	15	5.50	0.001



In Sweden, the most consistent decrease in male size measurements was found; all decreased significantly from before protection to afterwards. Females, however, only tended to decrease in all measurements except body weight. This result probably was affected by a small sample size before protection (Table 7).

In northern Norway all size measurements decreased significantly in both sexes from before protection to afterwards, except male condylobasal length (Table 8).

## Discussion

### Sex and age structure

Changes in densities of hunters and their behaviour probably accounted for the observed change in sex and age structure of the populations. Male wolverines normally disperse further from the denning area and have a larger home range than females (Krott 1959, 1982, Hornocker & Hash 1981, Bjärvall 1982, Magoun 1985, Whitman et al. 1986, Banci & Harestad 1990). Therefore, we expect males to be exposed to hunters more often than females. However, females are more readily exposed during the denning period if den sites are known beforehand. Wolverines have been protected during the denning period since 1973. During the period of protection, wolverines have been hunted only in specific areas where high losses of domestic sheep or domestic reindeer have been recorded. High sheep losses in summer are believed, and in some cases have been documented, to be the result of predation either by young males (Moe 1968) or by adult females and their cubs (Kvam & Sørensen 1981). An effect of protection resulting in increased densities in Sweden and southern Norway and the longer dispersal distance of young males is therefore a reasonable explanation for the skewed sex ratio towards more males in the material collected after protection. The restriction on hunting method and area could also explain why the age structure of females was skewed towards older animals after the enforcement of protection.

### Choice of size parameters

Because all large northern mammals depend on variable food supplies and because abundance of this food influences their body condition, we consider measurements of skeletal parts to be a better indicator of body size than body mass alone (e.g. Sæther & Haagenrud 1983). The choice of characters to measure depends on the questions posed (Radinsky 1984). One of the most commonly used size measurements is the condylobasal length of the skull, but Wiig's (1989) study indicated that skull profile length gave the best expression of general size for the wolverine. The wolverine has an extremely powerful bite relative to its body size (Krott 1982). In most carnivores the postor-

bital fibres of the *temporalis* muscle and the *zygomatico-mandibularis* muscle supply much of the bite force (Smith & Savage 1959, Ewer 1973, Moore 1981). Wiig (1989) found that the zygomatic arch is relatively more developed in the wolverine than in other mustelids, and concluded that in wolverines the *zygomatico-mandibularis* muscle is more important in generating a forceful bite than in other mustelids. Characters such as the profile length and zygomatic breadth, which are correlated with the attachment area and moment arm of the jaw muscle mass i.e. the *zygomatico-mandibularis* muscle, are important in the wolverine's life history and therefore useful as general size parameters.

### Density-dependence and food availability

Our analyses are based on animals collected over more than a century from a very large geographical range, within which habitats and densities probably varied greatly. The analyses are therefore coarse and the discussion must be on a broad scale. Nevertheless, our analyses showed geographical differences in size independent of temporal distribution and general trends in all geographical areas. Body size increased gradually in both male and female wolverines in the northern areas before they received protection, and declined strongly afterwards, also in southern Norway.

Wolverines were hunted to extremely low numbers, almost to extinction in southern Norway and Sweden (Myrberget & Sørungård 1975, Ahlén 1977). The hunting statistics from Sweden declined steeply in a regular manner from about 1870 until protection and the increase in male and female body sizes was quite consistent with year before protection. The hunting statistics from Norway indicated more pronounced fluctuations in population densities and less pronounced increases in body sizes here. The appearance of the largest wolverines in the two low-density areas and smaller animals from northern Norway in the period immediately before protection supports the food limitation hypothesis. Wolverines in southern Norway have lived in low-density populations for a long time, so we did not expect to find density-dependent effects here.

Wolverine foraging and hunting behaviour (Haglund 1966, Pulliainen 1968, Myhre & Myrberget 1975, Bjärvall & Isakson 1982, Banci 1987) and reproductive patterns (Myrberget & Sørungård 1979), suggest that wolverines are opportunistic feeders utilising a wide range of food sources. Bjärvall & Lindström (1991) speculated that the removal of the dominant predator, the wolf, from the Scandinavian boreal ecosystem has had a negative effect on wolverine density because less secondary prey is now available for the scavenging wolverine. This hypothesis, however, does not seem to offer an explana-



tion of our results as the wolf was absent almost throughout the entire period examined (Sørensen et al. 1986). However, it could explain at least partly, why the present distribution and densities seem to be more restricted now than at the turn of the century. It may also be argued that predators like wolverines should become larger in response to the disappearance of other large predators in this century, because the lack of secondary prey would make them more dependent on larger body sizes to kill their own prey. However, this argument has been proved wrong by the fact that body sizes declined after protection.

The decline in wolverine body size after protection in all areas could also reflect density-dependent changes in the population. But the present population is very small compared with that before the turn of the century (see Fig. 1).

In modern times, human activities have induced multifactorial changes in the Scandinavian boreal/alpine ecosystems since about the time when wolverine protection was enacted. The dramatically increased fragmentation and loss of habitat caused by roads, hydropower dams, recreational cabin building and associated traffic in mountainous areas should be taken into account when considering the possible differences between discontinuous and continuous wolverine populations. The distribution and home range size of solitary females is determined to a large extent by food availability (Sandell 1989), but will also be affected by human disturbance of critical female denning sites for a shy animal like the wolverine. This could strengthen the density-dependent effects because it introduces stress or, in the worst case, abandonment of denning sites.

Ungulate populations in Scandinavia have reached record numbers during the last decades, with an increase in numbers of wild and domestic reindeer since the protection of wolverines. Modern big game management throughout Scandinavia and reindeer husbandry in the southernmost herding areas, developed during the last two decades, may be expected to reduce the amount of food for wolverines in spite of the increase in number of potential prey. This is attributable to maximised turnover in managed ungulate populations resulting in less natural mortality and fewer old animals in poor condition available as prey for scavengers and less efficient predators like the wolverine.

It could also be argued that the increased sheep farming in Norway and the subsequent higher loss due to wolverine predation should result in more food supplies for the wolverine. Sheep are only in the system throughout the short summer period when the general food supplies are highest and are probably of little benefit to the wolverine, as indicated by our results.

We suggest that both the food supplies and availability

of appropriate habitat for the wolverine population have declined after protection. This may account for the apparent density-dependent effects on body size that we observed even with the much reduced present population densities compared with earlier. Competition for food resources may have increased relatively in relation to available habitat.

An alternative hypothesis is that the apparently impoverished contemporary wolverine habitat has fragmented the total Scandinavian wolverine population into several small and possibly isolated subpopulations (Kvam et al. 1988). If so, the effective breeding population sizes are very low. The decline in body size could then be a delayed effect of the loss of genetic diversity. Genetic diversity is closely related to the effective population size because the average proportion of heterozygous loci declines by a factor of  $1-1/2N$  per generation (Wright 1931). Until we know more about the effect of a "bottleneck" and low effective population sizes on the variance of wolverine population demography (Lande & Barrowclough 1987, Lande 1988), genetic problems cannot be ruled out as an additional factor affecting the wolverine in contemporary Scandinavia.

Our results suggest that protection of the wolverine alone is insufficient in the management of the wolverine population. A more holistic evaluation of the entire habitat complex may be necessary to ensure the continued recovery of the wolverine population, especially in southern Norway.

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