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Authors: Persson, Jens, Willebrand, Tomas, Landa, Arild, Andersen, Roy, and Segerström, Peter

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The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*

Jens Persson, Tomas Willebrand, Arild Landa, Roy Andersen & Peter Segerström

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Wolverine *Gulo gulo* populations have a low reproductive potential and are thus relatively sensitive to changes in survival rates. Consequently, knowledge about survival and mortality causes in juvenile wolverines is important for a sound management of the species. We estimated survival rates for juvenile wolverines and evaluated the relative importance of intraspecific predation compared to other mortality causes in northern Scandinavia during 1993-2001. We monitored 80 radio-marked juvenile wolverines from May to February. Intraspecific predation was the most important cause of juvenile mortality and occurred during two periods. First, seven juveniles were killed in May-June when still altricial, i.e. infanticide. Second, four juvenile females were killed by conspecifics outside their mothers' territories after independence in August-September. The survival rate of radio-marked juveniles during May-February was 0.68. There was a strong tendency for survival to be lower during the summer when juveniles were altricial, than after they became independent. The estimates of survival rates and mortality causes provided by this study are important for the understanding of wolverine population dynamics. Currently, our data are too weak to suggest an explicit explanation for infanticide in spring/early summer. Still, in the light of the available information on wolverine life history and infanticide patterns in other species, we suggest two, not mutually exclusive, hypotheses to consider for further investigation: 1) males kill non-related juveniles to increase their reproductive success, and 2) females kill non-related juveniles to reduce competition for resources. In addition, attention should be given to the alternative hypothesis that infanticide in wolverines is non-adaptive. Finally, we suggest that independent juvenile females were killed by resident females in territorial defence.

Key words: Gulo gulo, infanticide, intraspecific predation, juvenile survival, mortality causes, Scandinavia, wolverine

Jens Persson & Tomas Willebrand, Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden - e-mail addresses: jens.persson@szooek.slu.se (Jens Persson); tomas.willebrand@szooek.slu.se (Tomas Willebrand)
Arild Landa & Roy Andersen, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway - e-mail addresses: arild.landa@nina.no (Arild Landa); roy.andersen@nina.no (Roy Andersen)
Peter Segerström, Vaikijaur 617, S-962 99 Jokkmokk, Sweden - e-mail: peter.solbritt@jokkmokk.pp.se

Corresponding author: Jens Persson

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A prerequisite for sound carnivore management is solid knowledge about the factors affecting population dynamics. Only with such knowledge is it possible to responsibly manage populations and fulfil conservation goals (Fuller & Sievert 2001). Population modelling is an important tool in the understanding of population dynamics, and age-specific data on demographic rates and data on their variation are of crucial importance in this context (e.g. Boyce 1992, Beissinger & Westphal 1998).

Change in adult female survival is generally the single most important parameter for population growth of long-lived mammals (Stearns 1992, Boyce 1992, Roff 1992, Tuljapurkar & Caswell 1996). However, juvenile survival is often more variable than adult survival (e.g. Charlesworth 1994) and can have a stronger effect on population dynamics than reproduction or survival of older age classes (Eberhardt 1985, Stearns 1992, Caswell 1989, Charlesworth 1994).

Wolverine *Gulo gulo* populations have a low reproductive potential (Magoun 1985, Landa, Lindén & Kojola 2000) and are thus relatively sensitive to changes in survival rates (Weaver, Paquet & Ruggiero 1996). It is therefore important to estimate rates and causes of juvenile mortality to understand variations in population growth. Previous field studies have not been able to estimate survival rates in wolverine populations, and information on mortality causes is scanty, especially for juveniles (Banci 1994, Landa et al. 2000). However, several authors have hypothesised that infanticide might occur in wolverine populations (Banci 1994, Bjärvall, Danielsson, Franzén & Segerström 1996). Infanticide refers to killing of dependent (i.e. altricial) offspring, and is a potentially important source of selection in social systems (Janson & van Schaik 2000). Infanticide has been observed in several mammalian carnivores (Packer & Pusey 1984, van Schaik 2000b). In most species, males are the infanticidal sex (Hrdy 1979), but infanticide by females has been documented in more than 50 species belonging to five mammalian orders (Digby 2000) and several carnivore species (Wolff & Peterson 1998). It is important to reveal potential explanations for infanticide, as it can have important management implications (e.g. Swenson 2003).

Hrdy (1979) proposed four different adaptive explanations for the occurrence of infanticide; exploitation (food), resource competition, parental manipulation and sexual selection. An additional explanation is that infanticide is non-adaptive (Hrdy 1979, Ebensperger 1998). The sexual selection hypothesis predicts that killing of young, sired by other males, will increase the reproductive success of infanticidal males, typically by shortening the interval until the next ovulation in the mother (Hrdy 1979). Infanticide by males in a context consistent with the sexual selection hypothesis has been reported for 15 carnivore species (van Schaik 2000b). Resource competition is more closely linked to female reproductive competition. By killing the young of other females, an infanticidal female and her young will have fewer competitors for limited resources, both at present and in the future (Hrdy 1979, Hoogland 1995). Wolff & Peterson (1998) hypothesised that the primary function of territoriality in solitary and semi-social female mammals could be to protect vulnerable young from infanticidal conspecific females. Non-adaptive explanations for infanticide consider that infanticide is either maladaptive (i.e. pathological) or neutral (i.e. infanticide results from selection for some other behaviour; Ebensperger 1998).

In solitary carnivores, such as the wolverine, the period of highest juvenile mortality should be expected during the altricial stage, when females are facing a trade-off between the high energetic expenditures of lactation (Sadleir 1984) and protection of the cubs. Along with this, juveniles are likely to be most vulnerable to predation (not necessarily including consumption) during the period when they are left unattended in the natal den (March-April) and when they have just left the natal den (May-June; Magoun 1985, Landa, Strand, Swenson & Skogland 1997). A second major period of mortality could be expected to take place when the juveniles are forced to be nutritionally independent and leave the protective surroundings of their mothers in August-September (Vangen, Persson, Landa, Andersen & Segerström 2001).

In this study, we assess the relative importance of intraspecific predation compared to other mortality causes and discuss potential mechanisms explaining the occurrence of intraspecific predation upon juvenile wolverines. We present the first estimates of juvenile survival rates in wolverines. In addition, we present estimates of seasonal survival from May to independence in August, and from August to the age of one year.

Study areas

We carried out the study in and around the Sarek National Park in the county of Norrbotten, Sweden (Kvikkjokk: 67°00'N, 17°40'E) and in the southeastern part of the county of Troms in northern Norway (Dividalen: 68°50'N, 19°35'E). The climate is continental with cold winters (-10 to -13°C in January) and medium warm summers (13-14°C in July). The annual precipitation is 500-1,000 mm in both areas, except in the western part of Sarek

where it is higher (around 2,500 mm; Påhlsson 1984, Ryvarden 1997). The ground is usually snow-covered from October to May. Both areas are characterised by deep valleys, glaciers and high plateaus with peaks up to 1,700-2,000 m a.s.l. The valleys are dominated by mountain birch *Betula pubescens* and Scots pine *Pinus sylvestris*, and in Sarek also by Norway spruce *Picea abies* (Grundsten 1997). Mountain birch forms the tree line in both areas and reaches to a maximum of 600-700 m a.s.l. (Grundsten 1997, Ryvarden 1997). Semi-domesticated reindeer *Rangifer tarandus* are managed extensively by indigenous people (the Samis) in both study areas, and sheep are grazed during the summer in Troms. During 1998-2000 the minimum population size of ≥1-year-old wolverines in the counties of Troms and Norrbotten was estimated to be 72 ± 13 (SD) and 222 ± 40, respectively (Landa, Tufto, Andersen & Persson 2001).

Methods

Capture and radio-marking

We radio-marked 89 juvenile wolverines, 61 in Sarek during 1993-2000 and 28 in Troms during 1996-2000. Only animals marked before the age of six months were used in the analyses.

We captured and equipped most juveniles with transmitters at maternal dens or rendez-vous sites (Magoun & Copeland 1998) in late April to June when they were 2-3 months old. We captured eight animals later in the year together with their mothers (July: N = 6 and August: N = 2). We located juveniles either by locating a transmitter-equipped mother or by snow tracking non-marked females. We captured them by hand and immobilised them with Xylazin and Ketamin (Sarek) or Medetomidin and Ketamin (Sarek and Troms; Arnemo, Dypsund, Berntsen, Schulze, Wedul, Ranheim & Lundstein 1998). During the first years (1993-1995) we equipped 15 juveniles with transmitters glued to the fur (Telonics® Mod 055, Arizona, USA; weight: 31-34 g) and then later in the summer relocated and equipped them with collar-mounted radio transmitters (Telonics® Mod 315, Arizona, USA; weight: 150-200 g). From 1996 we equipped 74 juveniles with intraperitoneally implanted transmitters (Telonics® Imp/210/L, Imp/300/L or Imp/400/L, Arizona, USA; weight 30-90 g). Of the animals equipped with transmitters glued to the fur, nine lost their transmitter within one month after marking, and they were excluded from the analysis.

Survival and mortality causes

We monitored 80 juvenile wolverines, 52 in Sarek and 28 in Troms (Table 1). Of these, 48 had one sibling and 12 had two siblings. There were 32 litters in Sarek and 16 in Troms. Most litters came from mothers that only produced a single litter in the study period, i.e. 37 juveniles from 25 litters. Mothers producing two litters contributed with 22 juveniles in 10 litters, mothers producing three litters contributed with 14 juveniles in nine litters, and one mother producing four litters contributed with seven juveniles. Of all the juveniles, 39 (49%) were tracked past February, during their first year of life. However, more juveniles were monitored throughout their first year of life in Sarek (62%) than in Troms (25%).

We detected the death of radio-marked wolverines during bi-weekly radio-tracking from fixed-wing aircraft, in addition to supplemental ground tracking. When a mortality signal was detected, we investigated the site as soon as possible to determine the cause of death. The mean time lapse between the time when an animal was last heard alive and the time when the carcass was located was 17 days (range: 1- 62 days). All dead cubs recorded in the field were analysed post-mortem following Landa (1999). In most cases the cause of death was obvious. In five cases the cause of death was classified as unknown, because the cause could not be reliably determined. We defined all killings as predation, even when the animals killed had not been consumed. We estimated the time elapsed from the date when an animal was last heard alive until its death, based on an evaluation of the condition of the carcass and indications from the site of the carcass (e.g. signs in the snow). When the condition of a carcass indicated that the animal had been recently killed, we assumed the death to have occurred when 80% of the time between the last time when the animal was detected alive and the date when the mortality was detected had elapsed. If no indications were

Table 1. Number of juvenile wolverines captured and monitored in Troms and Sarek during 1993-2000.

Year	Sex	1993	1994	1995	1996	1997	1998	1999	2000	Total
Troms	♀	-	-	-	6	1	2	5	6	20
	♂	-	-	-	3	1	4	-	-	8
Sarek	♀	1	1	5	4	2	7	7	5	32
	♂	-	-	2	5	2	4	5	2	20
Total		1	1	7	18	6	17	17	13	80

available, we assumed the death to have occurred when 40% of that time (*cf.* Johnson 1979) had elapsed. We lost contact with marked wolverines in 18 cases, probably due either to radio failure, long-distance dispersal or illegal killing and destruction of the transmitter, and these were classified as lost.

Data analysis

To estimate survival rates, we pooled data from all years to obtain a sample size suitable for Kaplan-Meier estimates modified for a staggered entry design (Pollock, Winterstein, Bunck & Curtis 1989). However, even then, the number of juvenile wolverines in Troms was less than 10 individuals in December. Therefore, we could not extend the survival curve beyond 4 December for Troms. To further evaluate the data, we used the approach suggested by Heisey & Fuller (1985). Thus, when comparing survival between groups, we used days as units and calculated daily survival (Krebs 1999).

The probability of survival was compared between sex classes and study areas using Z-tests (Heisey & Fuller 1985). We analysed differences in mortality causes, proportion of surviving juveniles from litters of different sizes and different female categories, using the robust Fisher's exact test (Siegel & Castellan 1988). We performed all statistical analyses using SAS (SAS institute 1989).

Results

Mortality causes

Of the 80 juvenile wolverines, 22 died during the study (Table 2). The most important identified cause of death was intraspecific predation (50%; N = 11). Of these, seven were killed in May to early July and four were killed during August-September. Other confirmed mortality causes were legal harvest (18%; N = 4), illegal harvest (N =1) and traffic accident (N = 1). Mortality from unknown causes was 23% (N = 5). During June-July, four juveniles died from unknown causes, and in all these four cases only the transmitters were found. In one case, the transmitter was found at the same time and at the same place where a sibling was found killed, suggesting that this male and possibly some of the others were killed by conspecifics. The fate of 18 animals was unknown due to loss of radio contact, but circumstantial evidence suggests that at least one of them was illegally killed.

The proportion of known deaths among the marked juvenile wolverines did not differ between the two areas (Sarek 29%, Troms 27%), but more animals were lost in Troms (46%) than in Sarek (10%). The main reason for the high number of juveniles that were lost in Troms was periods of poor conditions for aerial radiotracking, coinciding with the timing when dispersal begins (Vangen et al. 2001).

The causes of death of juvenile wolverines were significantly different between Sarek and Troms, excluding lost animals and those who survived (Fisher's exact test: P = 0.011). In Sarek, 10 (19%) juveniles were killed by other wolverines, whereas only one (4%) was killed in Troms, but when considering only altricial juveniles killed by conspecifics between 10 May and 7 July, the difference was not significant (Fisher's exact test: P = 0.19). The proportion of juveniles that were killed by other wolverines was not significantly different (Fisher's exact test: P = 0.31) between the sexes (females 17%, N = 52; males 7%, N = 28).

Survival rate

The average first-year survival rate for juvenile wolverines was 0.68 (95% CI: 0.54-0.81) in Sarek (until 28 January), and 0.77 (95% CI: 0.49-1.0) in Troms (until 4 December). The difference in survival rates between the two study areas was not significant (Z = 0.36; P > 0.72). That allowed us to pool the data from the two areas, resulting in an average first-year survival rate (until 28 January) of 0.68 (95% CI: 0.56-0.80; Fig. 1).

In the analysis, we treated all juveniles as independent observations. However, three sibling pairs were killed by other wolverines or died from unknown causes in the same instance. This could bias the survival estimate to be lower than otherwise obtained. When exclud-

Table 2. Mortality causes of the 80 juvenile wolverines studied in Sarek and Troms during 1993-2000.

	Capture		Cause of death						
Area	Sex	N	Illegal harvest	Legal harvest	Traffic	Intraspecific predation	Unknown	Total	Animals lost
Sarek	♀	32	-	1	-	9	2	12	2
	♂	20	1	-	-	1	-	2	3
Troms	♀	20	-	2	1	-	2	5	9
	♂	8	-	1	-	1	1	3	4
Total		80	1	4	1	11	5	22	18

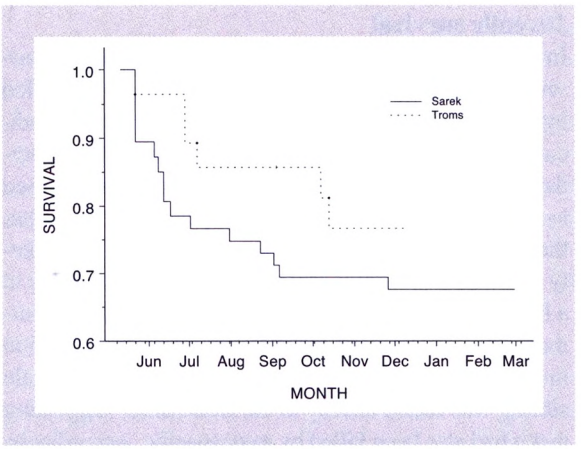

Figure 1. Monthly survival curves for radio-marked juvenile wolverines in Sarek and Troms during May-February 1993-2000.

ing the subsequent deaths of one sibling in each pair (N = 3) the survival rate until 28 January was 0.72 (95% CI: 0.60-0.84).

Male and female average first-year survival rate was 0.81 (95% CI: 0.63-0.99; N = 28) and 0.62 (95% CI: 0.46-0.77; N = 52), respectively. Males in Sarek showed a significantly higher survival rate than did females (0.89 and 0.56, respectively; $Z = 2.75$, $P < 0.006$).

The survival rate of juveniles showed a strong tendency to be lower during the altricial period (11 May - 31 July) than after independence (1 August - 28 February; T-test: $t = 1.90$, $P = 0.06$; Table 3). Of 22 cases of juvenile mortality, 13 (59%) occurred during May-July, six (27%) during August-October and three (14%) during November-February.

Discussion

Mortality causes

We showed that intraspecific predation was the most important cause of juvenile mortality in our study areas. This is the first documentation of intraspecific predation on juvenile wolverines. The causes of juvenile mortality in wolverine populations have previously been largely unknown (Banci 1994, Landa, Tufto, Franzén, Bø, Lindén & Swenson 1998). Documented death causes among four juveniles in North America were starvation and wolf *Canis lupus* predation (Hornocker & Hash 1981, Banci 1987).

Table 3. Survival of juvenile wolverines in Sarek and Troms during the periods 11 May - 31 July and 1 August - 28 February, based on survival of radio-marked individuals. Note that the two periods differ in length.

Period	No of days	Finite survival	Monthly survival
11 May - 31 July*	81	0.78	0.91
1 August - 28 February	212	0.81	0.98

* 11 May was the median date for marking of juveniles

Intraspecific predation occurred during two distinct periods. In May to early June, seven juveniles were killed when still dependent, i.e. infanticide. Considerably later, in August-September, four juveniles were killed, i.e. after independence. This suggests two different categories of intraspecific predation on young wolverines.

Both adult males and females could benefit from killing non-related dependent juveniles in late spring/early summer. Males could increase their reproductive benefit (sexual selection hypothesis) and females could decrease competition for resources (e.g. territories or denning areas). The death of an unrelated infant also reduces the net reproductive success of a competitor of the infanticidal individual (Hrdy & Hausfater 1984). We do not consider exploitation, parental manipulation and social pathology as probable explanations, as killed juveniles were left uneaten, parental manipulation is unlikely to occur after the most energy-consuming part of the offspring rearing and the high frequency of infanticide does not suggest social pathology (e.g. males or females killing their own offspring).

Sexually selected male infanticide has been suggested for wolverines (Banci 1994, Bjärvall et al 1996, Swenson 2003). However, because the wolverine is a seasonal breeder and most females mate every year (Banci 1994), the fitness benefit is not obvious for wolverine males. Still, male infanticide is shown in five other seasonal breeders (Bartos & Madlafousek 1994, van Schaik 2000a), and might confer a limited reproductive advantage to males if loss of offspring will increase the size or survival of the subsequent litter (Hrdy & Hausfater 1984, van Schaik 2000b). Consequently, the timing of the infanticide in relation to mating time is not as critical as for species in which the potential benefit is a shortened interval until the next ovulation in the mother. Only 40-60% of wolverine females reproduce every year (Landa et al. 1998), and the reproductive success of wolverine females is influenced by the cost of reproduction in the previous year (Persson 2003). Thus, infanticidal males might gain a reproductive advantage by improving the female's physiological condition the following season, especially if infants are killed during the period of maximal parental investment (Hrdy 1979), i.e. lactation in most mammals (Sadleir 1984). However, because most infanticide probably occurred after weaning, it is uncertain whether this would have a significant effect on the physiological condition of females.

Instead, infants should be killed earlier during the period of maximal parental investment (Hdry 1979). Nevertheless, feeding of fast-growing young after weaning might incur high enough costs on females to affect their condition the subsequent winter, thereby making infanticide a tenable strategy even some time after weaning. In conclusion, the earlier the cubs are killed, the larger the potential benefit would be for an infanticidal male.

What could a wolverine female gain by killing another female's progeny? She could decrease future competition for territories or denning areas for herself, and especially for her own progeny, by eliminating non-related progeny, i.e. future competitors. Female territoriality seems to be strongest during the period when they have altricial young (Magoun 1985, Landa et al. 2000; J. Persson, unpubl. data), which could be interpreted as a counterstrategy to female infanticide (Wolff & Peterson 1998).

Finally, infanticide could be the result of selection for some other behaviour. For example, it could be a by-product of male aggression during mating time (e.g. van Schaik 2000a). Because the observed infanticide coincided with the mating time, it cannot be excluded that at least some cases of infanticide result from general aggressiveness in males during mating time.

To summarise, current information is too weak to suggest an explicit explanation for infanticide in spring/early summer. Still, in the light of the available information on wolverine life history and infanticide patterns in other species, we suggest two, not mutually exclusive, hypotheses for further investigation: 1) males kill non-related juveniles to increase their reproductive success, and 2) females kill non-related juveniles to reduce competition for resources. In addition, attention should be given to the alternative hypothesis that infanticide in wolverines may have non-adaptive explanations.

The second category of intraspecific predation occurred during August-September, when four juveniles were killed. This coincided with the time of independence and increased movements outside the protective surroundings of their mothers (Vangen et al. 2001). All the juveniles killed during this period were females and they were killed outside or on the border of their natal home ranges. It is not likely that a male would kill a daughter or a potential mate. Resident females in our study areas seem to be territorial, especially during the offspring-rearing season (J. Persson, unpubl. data). We have documented an adult female being killed by another wolverine in our study area, possibly in territorial strife. Consequently, we suggest that the four juvenile females were killed by resident females in defence of territories.

Juvenile survival

In Sarek, male juveniles had a significantly higher survival rate than females; nine out of 10 juveniles killed by conspecifics in Sarek were females, which could indicate that females are more exposed to this type of predation. Indeed, female juveniles seem to be more exposed to intraspecific predation after independence. However, the sex bias in the early summer infanticide is most likely explained by a litter effect, e.g. all three juveniles in a litter with only females were killed in 1998. Furthermore, the only juvenile killed by intraspecific predation in Troms was a male and the transmitter from its male sibling was found nearby at the same time, suggesting that it had also been killed by a conspecific. Accordingly, a litter effect and a difference in vulnerability to intraspecific predation at the time of independence, may explain the higher mortality among female juveniles in Sarek.

As predicted, there was a strong tendency for survival to be lower during the period of dependence (May-July) than after independence. Presumably, juveniles are especially vulnerable during this period when they are left alone at rendez-vous sites while the female is hunting, and it was also during this period the infanticide occurred.

Conclusion

Our results show that intraspecific predation forms a substantial part of wolverine population dynamics, and thus makes it important to uncover the causal mechanisms behind infanticide in wolverines. This could be essential for our understanding of the effects of harvest on small wolverine populations, as carnivore control can affect net reproductive rates through its impacts on infanticidal behaviour by males (Frank & Woodroffe 2000). Such an effect is proposed for brown bears *Ursus arctos*, where killing of resident males seems to increase juvenile mortality in the following years (Swenson, Sandegren, Söderberg, Bjärvall, Franzén & Wabakken 1997), and has been suggested for several other carnivore species as well (Swenson 2003). This is potentially important because wolverine hunting regulations sometimes have different quotas for the sexes.

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