Oecologia (2003) 137: 370–376
DOI 10.1007/s00442-003-1373-6

POPULATION ECOLOGY

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An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer

Received: 14 May 2003 / Accepted: 4 August 2003 / Published online: 4 September 2003

Abstract A central issue in ecology is to what extent food limitation and predation affect animal populations. We studied how survival and reproductive success was related to the female's size in a population of semi-domesticated reindeer during 2 years where there was a large difference in snowfall during winter. The females were kept within a predator-free enclosure for about 5 weeks during the calving period and thereafter released to their natural summer pastures. Small females were more likely to fail to reproduce and they produced smaller calves than large females. Additionally, small females were more likely to loose their calves due to starvation within the predator-free enclosure and to predators outside the enclosure. Food limitation during the harsh winter appeared to be the major cause of deaths. However, food limitation interacted with predation and led to high calf losses when the females experienced low food availability during the harsh winter. In contrast, predators killed no calves after the mild winter. Apparently, the interaction between predation and food limitation is due to small females favouring their own growth and survival over calf production in summers following harsh winters with food shortage. Our results indicate that a compensatory relationship exists between mortality due food limitation and predation. Thus, the impact of calf predation on reindeer demography and population dynamics may be limited.

Keywords Body weight · Costs of reproduction · Demography · Life history strategies · Predator-prey interactions

Introduction

In ungulates, the costs of reproduction are related to the female's size (Clutton-Brock 1984; Saether et al. 1996). Small individuals are less likely to produce offspring (Cameron and Ver Hoef 1994; Sand 1996; Saether et al. 1996) and their offspring also have a low probability of survival (Clutton-Brock et al. 1996). A number of recent studies have provided information about how winter climate and animal densities affect the weight and, in turn, the demography and population dynamics of ungulates [moose *Alces alces*: Saether and Gravem (1988); Saether and Heim (1993); Saether et al. (1996); Sand (1996); red deer *Cervus elaphus*: Clutton-Brock (1983); Albon et al. (1987); Clutton-Brock et al. (1987a, 1987b, 1988); Coulson et al. (1997); roe deer *Capreolus capreolus*: Gaillard et al. (1992, 1996, 1997); Andersen and Linnell (1998); Pettorelli et al. (2002); bighorn sheep *Ovis canadensis*: Festa-Bianchet et al. (1997, 1998); Festa-Bianchet (1998); Soay sheep *O. aries*: Clutton-Brock et al. (1992, 1996); Coulson et al. (2001)]. When population size increases, the competition for food among individuals increases, leading to reduced weight gain in summer and increased mass loss in winter. Similarly, an unfavourable climate reduces the quality or quantity of food available, which also reduces weight gain during summer and increases mass loss during winter. Such events may even lead to die-offs of small individuals outside their prime age (Gaillard et al. 1998, 2000).

Winter climate also affects mortality of ungulates due to predators. Losses to coyote (*Canis latrans*), mountain lion (*Puma concolor*) and wolf (*C. lupus*) increase in winters with heavy snowfall (Verme 1968; Del Giudice 1998; Patterson and Messier 2000; Mech et al. 2001; Del Giudice et al. 2002; Jedrzejewski et al. 2002). The risk of predation also increases over the course of the winter as the individuals' nutritional status deteriorates (Del Giudice et al. 2002; Jedrzejewski et al. 2002). Accordingly, it has been suggested that the probability that a predator kills an individual is dependent on the prey's nutritional status (Del Giudice 1998; Smith et al. 2000). Furthermore, it is shown

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that unfavourable snow conditions that reduce food availability in winter may increase predator vulnerability of calves born in the following summer (Adams et al. 1995; Singer et al. 1997).

Generally, the interaction between food limitation and predation is poorly understood (see review in Linnell et al. 1995), but harsh weather or high animal density, causing food limitation, may be expected to result in a compensatory relationship between food limitation and predation. That is, increased mortality caused by predators may reduce the mortality due to starvation, keeping the overall mortality rate, as well as the recruitment to the population, constant (Bartmann et al. 1992).

In Fennoscandia, wolverine (*Gulo gulo*), lynx (*Lynx lynx*) and golden eagle (*Aquila chrysaetos*) may be important predators of reindeer (*Rangifer t. tarandus*) (Bjärvall et al. 1990; Landa et al. 1997; Sunde et al. 2000; Nybakk et al. 2002), but little is known about the interaction between climate, the individuals' nutritional status and the levels of predation by these predator species. In the present study, we examine to what extent survival and reproductive output of semi-domesticated reindeer in Finnmark, northern Norway, may be attributed to food limitation and predation during 2 years with large differences in food availability during winter. We kept the females in an enclosure for about 5 weeks during the calving period and released the females, plus their calves, to their summer pastures after calving. The animals were weighed and the calves fitted with radio transmitters on release from the enclosure. This procedure allowed us to test if female size has: (1) positive effect on female survival during late spring and calving; (2) a negative effect on the frequency of stillbirths, and (3) a positive effect on calf survival during the first days post-parturition in a predator-free environment, as well as their later survival in the presence of predators. If calf survival is independent of the females' nutritional status, then the size of females that lost their calves to predators outside the enclosure should be similar to those with surviving calves. If losses to predators interact with food limitation, then we expect calf mortality to occur inside the enclosure as well, and small females should be most likely to lose their calves to predators.

Materials and Methods

The study was carried out from May 2000 to July 2001 in a reindeer herd that has its winter pasture in the municipality of Kautokeino (69°00′N, 23°30′E), and its summer pasture in nearby Burfjord (69° 55′N, 22°00′E), northern Norway. The average snow depth in March and April was 168 cm in 2000 and 78 cm in 2001 in Tromsø (69°39′ N, 18°56′E). Deeper snow is known to negatively affect the calf production in our study area (T. Tveraa, unpubl. data).

In April, the animals are herded approximately 130 km from the winter pastures to the summer pastures where the females calve. For the first month or so after calving, the animals are located on a 7×7 km peninsula. When the temperature increases in July, the reindeer naturally migrate up into the mountains and towards the winter area, presumably in order to avoid insects (Folstad et al. 1991). To reduce the negative impact of the poor feeding conditions due to the heavy snowfall during winter 2000, the animals were transported from Kautokeino to the summer pastures. In 2001, when the feeding conditions were much better at the winter pastures, the animals were herded from the winter to the summer pastures using snowmobiles. The herd is free ranging in the summer and is only gathered for a day or two in large outdoor fences to mark the calves, and before moving in and out of the winter pastures.

The animals were fed with hay, lichen *Cladina* sp. and commercial pellets specially designed for reindeer from early April. During calving, the females were kept in an enclosure of approximately 0.5×0.3 km and fed daily with 1.0–2.5 kg pellets per female, plus lichen. In order to reduce competition between the individuals, the forage was distributed in several cradles (three individuals per cradle). In the beginning, most of the diet consisted of lichen, but the amount of pellets was gradually increased and was by far the major forage during the calving period. The females were kept in the enclosure from 2 May to 10 June in 2000 and from 8 May to 9 June in 2001.

In 2000 we weighed 138 females of which 6 died in the enclosure, 42 miscarried, 13 were barren, 14 lost their calf shortly after parturition, and 63 left the enclosure with a calf at foot. Females that miscarried, or lost their calf during their stay in the enclosure, were weighed and released from the enclosure between 19 May and 10 June, whereas those with a calf were weighed and released on 4 or 10 June. In 2001, no females died or miscarried during the stay in the enclosure. We weighed 35 females, of which two were barren, two lost their calves shortly after parturition, and 31 left the enclosure with a calf at foot. These 35 females represent a random sub-sample of the total herd. Because we were unable to separate females that miscarried from those that were barren in 2000, we combine these two groups and refer to them as miscarried in the subsequent sections. Moreover, in order to measure the mass change of reproducing and non-reproducing females, we weighed a random sub-sample of the animals again on 2 February 2001.

During daily visits to the enclosure, we registered calving and calf survival, but we were unable to register the calving dates of individual females in 2000. Calving dates in 2000 therefore refer to observations of newborn calves that were wet or not yet able to walk.

On release from the enclosure, the females were individually marked with a small tag in one ear, and weighed (±0.1 kg) with an electronic balance (Avery Berker, UK) specifically designed to weigh live reindeer. The calves were individually marked with a mortality transmitter (Sirtrack Inc., New Zealand) attached with an expandable neck collar. However, in 2000, 18 calves were too small (mean weight 4.7±0.2 kg) to be fitted with mortality transmitters, leaving 45 individuals (mean weight 7.2±0.26 kg) with transmitters. Thus, the weakest calves were probably excluded from our study. Therefore, this probably led to an underestimate of mortality rates in 2000. All calves were successfully reunified with their mothers before release to the summer pastures.

During the 30 days following the release of the animals, we searched daily for radio signals that could indicate dead calves using a Field-Master, FM-100, receiver (Advanced Telemetry Systems, Inc., USA) with a Yagi-III antenna (Sirtrack Inc., New Zealand). Dead calves were collected within 2 hours from the time we first recorded a signal from the radio transmitter and autopsies were carried out immediately.

Three predators, golden eagles, lynxes and wolverines, have been reported to kill reindeer calves in the study area (Anonymous 2000). In addition, the red fox *Vulpes vulpes* has been observed to kill calves. The different predators have different killing techniques and autopsy may separate kills of the different predator species (see Bjärvall et al. 1990 for a detailed description). The golden eagle mostly attacks the back of calves and the claws puncture vital organs. Autopsy reveals claw marks through the skin and into the body. The lynx may kill calves without any noticeable marks of attack at first sight. Autopsy reveals perforation of the throat from the canines and marks of the claws can be found on the back of the prey. The wolverine attacks the neck and the mane. Reindeer killed by wolverine are roughed up and bones are often crushed.

Sometimes the head is removed. The red fox also attacks the neck, but their bite is smaller and weaker, and bones are not crushed.

After the harsh winter (2000), we found ten dead calves during the first 3 weeks after release from the enclosure. Predation appeared to be the major cause of mortality as 83% of the known deaths were caused by predators: one was classified as killed by red fox, two by lynx, two by wolverine, and one died with no sign of any predator attack. In the remaining four cases, we found only the transmitter and small parts of the calves, such as the intestines. It was therefore not possible to determine the cause of death. Additionally, we found the remains of eight calves that were too small to be fitted with mortality transmitters when tracking the signals of one transmitter down the fox's den, and one transmitter was located in a steep cliff. Because we were unable identify these calves to their mothers, we did not include them in our analyses of calf mortality. Because the total sample is small and the death of some calves is unknown, we have classified the calves as either killed or survivors.

The data were organised and statistically analysed using SAS software (SAS Institute Inc. 1990). Throughout the analyses we checked the validity of the statistical models by examining residuals and influential values (e.g. Schlotzhauer and Littell 1991). Following this procedure, we removed one observation from the data. This was the weight and calving date of a calf that was born on 3 May 2000, weighing 14 kg on release in June. Moreover, one calf eluded weighing. The body masses of females and calves were examined using analyses of variance and covariance and calf survival was analysed using logistic regression with a binary response variable (survived or died) and the logit link function (Allison 1999). Values represent estimates with 95% confidence intervals. Tests are two-tailed and $P<0.05$ is regarded as statistically significant.

Results

Body mass, survival and reproduction

Calving was 6.4 days earlier [3.5, 9.4] and the calves 6.1 kg heavier [5.3, 7.0] after the mild winter (2001) compared to the harsh winter (2000). Similarly, the females were 9.4 kg heavier [6.4, 12.4] in 2001 than in 2000. None of the radio-collared calves ($n=31$) died during the 30 days following release from the enclosure in 2001, but in 2000, 10 of the 45 radio-collared calves died during this period.

Females that died during the stay in the enclosure after the harsh winter (2000) were on average 5.5 kg smaller [−0.07, 10.8] than those that miscarried, which were 5.4 kg smaller (1.7, 11.4) than those that lost their calves during the first days after calving. In contrast, females that lost their calves inside the enclosure did not differ in size from those that lost their calves outside the enclosure (mean difference 0.9 kg [−4.3, 6.1]). Females with a calf at foot when the study ended were 5.8 kg heavier [1.3, 10.3] than those that lost their calves outside the enclosure (Fig. 1). After the mild winter (2001), no females died, only two females were barren, and only two females lost their calves during the first days after calving. Because only four out of 35 individuals did not leave the enclosure with a calf at foot, we do not present any statistics for these individuals.

A large proportion of the variation in the calves' weight was explained by annual variation, but the females' weight also positively influenced the calves' weight (Table 1, Fig. 2). The sex of the calves did not, however, explain a significant proportion of the variation in weight (Table 1).

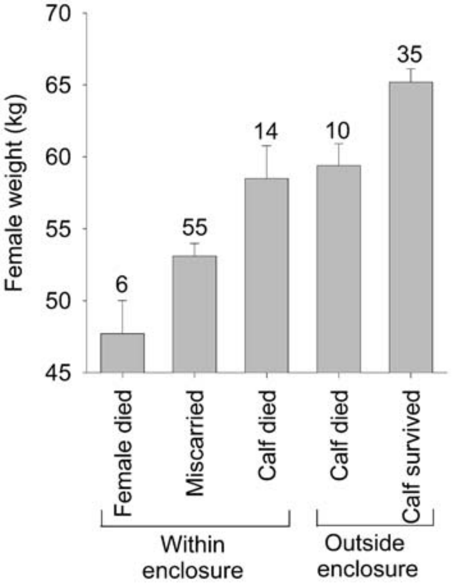

Fig. 1 The average weight (+SE) of female reindeer that died, miscarried or lost their calf within the enclosure, the weight of females that lost their calf outside the enclosure and of those that had surviving calves. Data are from 2000

The ten radio-collared calves that died outside the enclosure after the harsh winter had smaller mothers than those that survived (Table 2, Fig. 3). Neither the sex of the calf nor the weight of the calf significantly improved the fit of the model. However, the calves' weight was related to that of their mothers and inclusion of one of these variables is likely to mask the effect of the other. Accordingly, survival was positively related to the calves' weight ($\beta=0.56$ [0.03, 1.24]) when the mothers' weight was omitted from the model. The marginal interaction between sex of calf and female's weight (Table 2) was due to a stronger impact of female weight on survival of male than female calves. However, altogether only six out of 25 male and four out of 20 female calves died. After the mild winter (2001), none of the calves died during the first 30 days after release from the enclosure.

Table 1 Analysis of covariance for weight of reindeer calves, including the effect of year, the mother's weight and the calf's sex

Terms	Coefficient (±SE)	*F*	*df*	*P*
Year (2001–2000)	5.7±0.4	195.5	1	<0.0001
Mother's weight	0.12±0.03	14.8	1	<0.001
Residual			85	
Total			87	
Excluded terms				
Year×mother's weight		1.8	1	0.18
Calf-sex		1.8	1	0.19
Calf sex×mother's weight		0.8	1	0.37

Table 2 Logistic regression relating the survival of reindeer calves during the first 30 days after release from the enclosure to the calves' and the mothers' weight, and the sex of the calf. Data are from the harsh winter (2000) only as no calves died after mild winter (2001). Hosmer and Lemeshow's test indicated that the fit of the final model was good (χ^2=2.1, *df*=7, *P*=0.95)

Terms	Coefficient (±SE)	Deviance	*df*	Δdeviance	Δ*df*	*P*
Intercept	−11.7±4.9	47.7	44			
Mother's weight	0.21±0.08	39.1	43	8.6	1	<0.001
Excluded terms						
Calf's weight				1.1	1	0.30
Calf sex				0.1	1	0.78
Calf's weight×calf sex				2.5	1	0.12
Mother's weight×calf sex				3.6	1	0.06

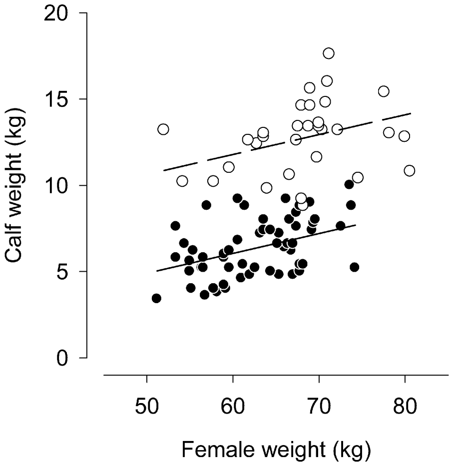

Fig. 2 The relationship between calf and female weight in reindeer in 2000 (*closed circles* and *solid line*) and 2001 (*open circles* and *dotted line*)

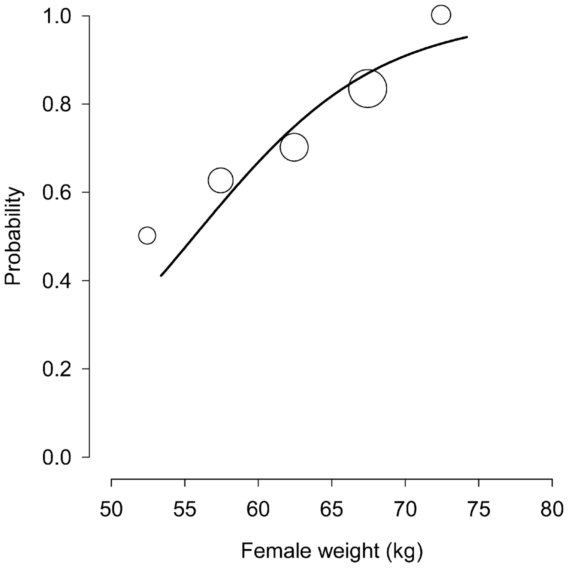

Fig. 3 The probability that a calf would survive the first 30 days after release from the enclosure in relation to the weight of the female. The *line* represents the estimate from a logistic regression model (see Table 2). The *circles* represent the frequency of calves surviving within each 5 kg interval. Data are from summer 2000

Costs of reproduction

Females that produced calves in 2000 were larger in the summer than those that failed, but they gained 13.5 kg less [10.4, 16.6] during the late summer and fall. An analysis of covariance with summer weight as the covariate (β=0.63 [0.47, 0.80]) demonstrated that those that produced calves weighed 8.5 kg less [5.9, 11.1] in the following winter than those that failed. The slopes were similar (difference in slopes; failed-reproduced: β=0.08 [−0.31, 0.48]), so we removed the interaction term from the final model (Fig. 4).

Discussion

This study demonstrates some of the mechanisms as to how food limitation and predation interact and cause death in reindeer. The females' ability to survive and successfully reproduce was positively related to their size (Fig. 1) and large females produced larger calves than small females (Fig. 2). Previous studies of reindeer and caribou

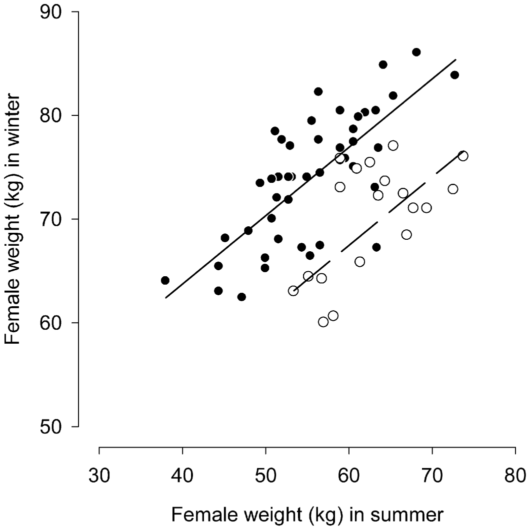

Fig. 4 The relationship between weight in summer 2000 and in the following winter (2001) of females that raised calves (*open circles* and *dotted line*) and those that miscarried or lost their calves shortly after calving (*closed circles* and *solid line*)

have also shown that large females are more likely to reproduce and produce larger calves than small females (Lenvik 1988; Lenvik and Aune 1988; Lenvik et al. 1988; Cameron and Smith 1993; Kojola 1993, 1997; Cameron and Ver Hoef 1994; Rönnegård et al. 2002). A positive relationship between the parent's size and access to food, and ability to successfully raise offspring, seems to be a general pattern in both mammals (e.g. Clutton-Brock et al. 1996; Saether 1997; Lummaa and Clutton-Brock 2002) and birds (e.g. Weimerskirch 1990; Chastel et al. 1995; Wendeln and Becker 1999), i.e. in species where most of the individual-based studies have been performed.

After the harsh winter, the females' nutritional status was poor, calving was delayed, the smallest females died before calving, and a large proportion of slightly larger females produced stillbirths. Several of the females that produced stillbirths were clearly exhausted after the delivery and they were mostly lying for several days before they recovered (T. Tveraa, unpubl. data). Similarly, it took several days for the smallest newborn calves to gain the strength necessary to follow their mothers, suggesting that small females and calves were highly vulnerable to predators. A critical question is whether this may have lead to a compensatory relationship between food limitation and predation. That is, whether calves killed by predators would have recruited to the population in a predator-free environment (Bartmann et al. 1992). Following the distribution of known deaths, predators killed eight of ten calves. However, it was the smallest females that lost their calves to predators after release from the enclosure (Fig. 3). Moreover, females that lost their calves to predators outside the enclosure were of a similar size to those that lost their calves inside the predator-free enclosure (Fig. 1), suggesting that these calves would have died due to food limitation in the absence of predators. This strongly suggests that there is a compensatory relationship between food limitation and predation. What should be noted is that literature reviews on calf mortality have failed to find any conclusive evidence towards a compensatory relationship between food limitation and predation (Linnell et al. 1995). However, studies carried out on wild ungulates have been unable to investigate the impact of maternal size on calf predation. Thus, an important trait reflecting the mother's ability to care for her calf has been missed. Moreover, our study is, to our knowledge, the first where it has been possible to compare the size of females that lose their calves in the presence and absence of predators within the same study season and population.

Another interesting result with respect to a compensatory relationship between food limitation and predation is the interaction between winter severity, maternal size, reproductive success and predation rates. Following the harsh winter, 22% of the calves attached with mortality transmitters were found dead during the first month after release from the enclosure. Following the mild winter, when the females' nutritional status was good, and only a few females did not leave the enclosure with a calf at foot, no calves were killed by predators during the first month after release from the enclosure. This is despite the fact that the red fox den, where we found several killed calves in 2000, was still occupied in 2001. We also know that at least one wolverine was present in the study area (T. Tveraa, unpubl. data). Apparently, food limitation during late winter, either through increased density (Skogland 1985), or heavy snowfall (Adams et al. 1995) greatly increases the predation risk of reindeer and caribou calves in the following summer (Adams et al. 1995; this study). In our study area, however, the calves killed by predators would apparently die even in the absence of predators, suggesting that the impact of calf predation on the demography and population dynamics of reindeer is limited, given the present predator fauna.

Why, then, were small females more likely to lose their calf? This may be understood by comparing the weight change of females that successfully reproduced with those that failed. Females that successfully reproduced gained less weight during the late summer and autumn, and were smaller in the following February, than those that failed to reproduce (Fig. 4). Similar results have been obtained in studies of bighorn sheep (Festa-Bianchet et al. 1998) and red deer (Mitchell et al. 1976). In reindeer and caribou, weight in the autumn and mid-winter is a good predictor of reproductive performance in the following summer, and small females are unable to successfully raise calves (Lenvik and Aune 1988; Cameron and Smith 1993; Cameron and Ver Hoef 1994). As judged from our study, small females are also at greater risk of dying during harsh winters. A small female reindeer that successfully delivers a calf is thus set at two options. On the one hand, she may invest in her calf, but this will be at the expense of her own mass gain and her own survival may thus be at risk if the following winter is harsh. On the other hand, the female may favour her own mass gain during the summer and autumn. This may greatly increase her prospect of surviving and successfully reproducing next year if the winter turns out to be good. In particular, young individuals, with many future breeding chances, are expected to be reluctant to invest in current reproduction at the expense of future reproduction (Charlesworth 1980; Stearns 1992). Unfortunately, we do not know the age of our study females. Nevertheless, since these are semi-domesticated reindeer, we may expect the herders to selectively remove old individuals (cf. Weladji et al. 2002), suggesting that that the small females that failed to reproduce were young individuals.

Acknowledgements We thank the Directorate of Nature Management, the Reindeer Husbandry Research Council and the County Authorities of Finnmark and Troms for financial support. Per A. Baehr and his family helped immensely with the fieldwork. Three anonymous reviewers, I. Folstad, J.-M. Gaillard and R. Aanes gave helpful comments on the manuscript.

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