

Induced orphaning reveals post-weaning maternal care in reindeer

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Received: 10 January 2011 / Revised: 11 November 2011 / Accepted: 25 January 2012 / Published online: 11 February 2012
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Abstract A common by-product of human harvesting is orphaning of calves in autumn. Despite this, there are few studies in northern and temperate ungulates evaluating the fate of orphaned calves and the potential benefits to offspring and costs to mothers of post-weaning maternal care. We manipulated orphaning and forage distribution during winter for two herds of reindeer (*Rangifer tarandus*): one nonfed and the

other supplementally fed to increase level of interference competition. Both herds consisted of females with and without calves at heel and orphaned calves. We measured survival and somatic losses during winter and distances between mother–calves and adult females–orphans within the herds. All females survived the winter, and there was no evidence of post-weaning maternal cost in terms of female’s mass loss. The winter mortality among calves was negligible and did not differ between orphans as compared to nonorphans. However, nonorphaned calves lost less mass and stayed closer to their mothers than orphans to adult females, suggesting that increased mortality might occur in harsher winters. This tended to be more marked in the fed group where interference competition was more likely due to feed being concentrated both in space and time. Reduced mass loss in nonorphans is therefore most likely due to mothers sharing and defending feeding resources and protecting their offspring from harassment by other herd members during their first winter. We conclude that hunting practise of northern and temperate ungulates where females having calf/calves at heel are intentionally or non-intentionally harvested, may have demographic side effects at least in harsh winters.

Communicated by P. Acevedo

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Keywords Feeding regime · Management induced orphaning · Post-weaning maternal care · Post-weaning maternal cost · Reindeer · *Rangifer tarandus*

Introduction

One of the classical and most studied life history trade-off is the one involving current versus future reproduction (Stearns 1992). Mothers should cease investing in their offspring when the costs of maternal care exceed the benefits of future reproductive success (Stearns 1992). This is clearly expressed in

seasonal environments where timing of reproduction is critical for the current year's offspring survival as well as for the start of next year's offspring (Clutton-Brock et al. 1983). Indeed, for iteroparous large mammals at northern latitudes, the intensity and duration of parental care is a crucial life history trade-off (Stearns 1992).

In ungulates, maternal effort related to lactation is normally high (Oftedal 1984) and costly (Clutton-Brock et al. 1983). Weaning time, when the direct transfer of energy and nutrients from mother to offspring is halted, is therefore a key life history parameter (Trivers 1974; Godfray 1995). Obviously, delayed weaning could benefit the current year's offspring, but at the cost of future reproduction (Hogg et al. 1992; Bårdsen et al. 2008; Langvatn et al. 2004; Holand et al. 2006). Festa-Bianchet et al. (1994) actually showed that the effect of early weaning in bighorn sheep (*Ovis canadensis*), a highly sexual size dimorphic ungulate, was sex-specific; male orphans were smaller as yearlings and at 4 years as compared to nonorphans, whereas no effect of female orphans versus nonorphans was found.

Even though calves are weaned in fall, they normally stay together with their mother during their first winter (Lent 1974), but few studies have examined maternal care after physiological weaning. Whether such post-weaning associations (Guinness et al. 1979; Gates et al. 1986; Skogland 1989; Green et al. 1989; Festa-Bianchet 1991) involve benefits to the offspring and whether it has a cost to the mothers is disputed (Green et al. 1989; Kojola 1989; Clutton-Brock 1991; Brookshier and Fairbanks 2003). Understanding the dynamic of post-weaning maternal care is especially important due to its applied consequences, as most large ungulate populations are harvested and females are often shot intentionally to regulate population numbers (Milner et al. 2006) or unintentionally (Markgren 1975).

Several studies have reported adverse effects of induced orphaning in white tailed deer (*Odocoileus virginianus*); reduced survival and home range size in fawns of both sexes (Giuliano et al. 1999) and increased spring and early summer emigration in female fawns (Etter et al. 1995). In contrast, Woodson et al. (1980), found no adverse effects, whereas Hölzenbein and Marchinton (1992) uncovered higher survival and lower emigration rates for orphaned as compared to nonorphaned male white tailed deer fawns. Jolicoeur and Crête (1988) reported no overall difference in winter survival of orphaned and nonorphaned moose (*Alces alces*) calves during three consecutive winters. Joly (2000) revealed lower survival rates of orphaned caribou calves. However, the weakness of this study is that orphans versus nonorphans were compared across different winters. These discrepancies indicate that the effect of orphaning maybe condition dependent, i.e., time of orphaning, sex-specific, winter severeness and location (e.g., density, habitat productivity, resource distribution) of the studied

populations. Also, the time scale (i.e., the length of surveying period after orphaning) could affect the outcome and hence the interpretation of the results.

Furthermore, the effect of orphaning may depend on the species social organization. In flock-dwelling species, there is evidence for orphaned calves being lowest in rank (Giovengo and Waring 1991). This will make them susceptible to harassment from other herd members, which may influence their feed intake negatively. Indeed, feeding efficiency and feeding time may differ according to rank (Barrette and Vandal 1986). This will be expressed even more clearly at supplementary winter feeding sites (Veiberg et al. 2004), which has been extensively introduced in northern environments as a counter measurement to dampen the negative effect of climatic winter stochasticity (Putman and Staines 2004). Furthermore, low ranked individuals, including orphans, will often be found in the periphery of the herd (Green et al. 1989), which potentially render them prone to predation.

Reindeer/caribou is a highly gregarious alpine/arctic ungulate (Geist 1999). Their winter feeding resources are patchily distributed (Klein 1996). The high energy expenditure of cratering (Fancy and White 1985) gives a strong incentive to gain, defend and maintain access to the resource (Skogland 1989). Indeed, craters are by far the most disputed resource among reindeer/caribou (e.g., Barrette and Vandal 1986; Kojola 1989; Skogland 1989). Espmark (1964) argued that reindeer calves are partly dependent on their mothers for their survival during the first winter of life, which they may attain by sharing craters with their mothers. Actually, in reindeer also females possess antlers, which are thought to be related to benefit in competition for feeding craters (Schaefer and Mahoney 2001). This underlines the potential functional importance of post-weaning maternal care and hence the possible negative effect of orphaning in reindeer, but evidence from manipulations are lacking.

We manipulated orphaning by moving calves between two large enclosures in an experimental reindeer herd and addressed the following questions: (1) Is there evidence for post-weaning maternal care during winter, i.e., do orphans experience reduced survival, increased body mass decay or stay farther away from adult females in the herd as compared to nonorphans? (2) Is there evidence for post-weaning maternal costs, measured as increased mortality and somatic losses among females having calf at heel, during the same period? (3) Does increased interference competition (by manipulating the concentration of the food resource in space and time) increase post-weaning maternal care and/or costs?

Study area

The study was conducted at Kutuharju Field Reindeer Research Station, in Kamaanen, Finland (69° N, 27°E).

The experimental reindeer herd at the Station amounts to around hundred winter animals which are free ranging within large seasonal grazing enclosures (altogether ~40 km²) (Holand et al. 2006; Røed et al. 2007; Mysterud et al. 2009). Birch (*Betula* spp.) and pine (*Pinus sylvestris*) forests with numerous lakes and bogs dominate the habitat with some alpine ridges at higher elevations. In this study, we use two enclosures: Piskivaara (nonfed), a rather lichen-rich pasture (about 800 kg DM/ha) that is about 10 km², and Lauvuvaara (fed), a lichen-poor pasture (about 300 kg DM/ha) about 14 km² (Kumpula, unpublished data)

Methods

Data

On January 7, 2009, all animals were rounded up. We manipulated calf status to produce females with and without a calf at heel (to estimate potential costs to maternal care), and orphaned and nonorphaned calves (to estimate benefits of maternal care, or costs of orphaning). Females without calves and orphans were established by slaughtering calves in December and by physically separating mothers and calves into different enclosures. All animals were weighed (to the nearest 0.1 kg) using a modified crate scale. A randomized-stratified approach according to females' initial body mass and age was performed to make sure that the mean initial body mass and age within each group are as equal as possible at start of the experiment. Females (with and without calf) with more or less equal body masses and age were randomly allocated to the two groups. The orphans followed accordingly. The nonorphaned were drawn randomly according to body mass and sex and allocated to the two groups. Finally, the animals were let onto the nonfed and fed site, respectively (Table 1).

The fed herd was daily string supplementally fed with concentrate (PoronHerkku, RehuRaisio) and silage. The mean average daily supplementary ratio amounted to around 500 g concentrate and 200 g hay/day per animal (Mika Tervonen, personal communication), accounting for about half of their estimated daily required winter-energy intake for maintenance, which has been measured to around 500 kJ/kg 0.75/day (reviewed by Hudson and Christopherson 1985). Before release, altogether 54 animals—five fed and six nonfed orphans and five fed nonorphaned calves and six nonfed, in addition to 16 females having calves at heel (12 fed and four nonfed) and 16 females without calves at heel (12 fed and four nonfed)—were equipped with Global Positioning System (GPS) collars to record geographical locations every 30 min. On March 16, the animals were again rounded up and weighed and the GPS collars dismantled and the stored GPS locations tapped. Two GPS collars (one calf and one female) had to be dismantled due to repeated snow build-up around the battery unit which hampered the foraging activity. In addition, due to problem with GPS data, the female–calves distance dataset included only eight orphans and eight nonorphan calves, seven from the supplemental feeding site and nine from the natural pasture.

Distance data

We used a Great Circle longitude–latitude calculations tool (<http://www.cpearson.com/excel/LatLong.aspx>) to assess the distance between a pair of individuals at a given time. The tool uses the following formula to estimate the distance between two locations (1 and 2) based on their GPS coordinates (i.e., using the latitude and the longitude of the two locations), where “R” stands for radians, “Lat” for latitude and “Long” for longitude:

$$\text{Radius Earth} \times 2\arcsin \left(\sqrt{\sin \left(\frac{R(\text{Lat}1) - R(\text{Lat}2)}{2} \right)^2 + \cos(R(\text{Lat}1)) \times \cos(R(\text{Lat}2)) \times \sin \left(\frac{R(\text{Long}1) - R(\text{Long}2)}{2} \right)^2} \right)$$

We estimated the distance between any calf and her mother at 12.00 every day of the month of February, as well as the distance between those same females and the orphans at the same day and exact same time. The distances obtained were then organised and used to estimate the average distance between all mother–calf pairs as well as average orphans–adult females distances for the two groups (nonfed and fed). This gave us two sets of distances: mother–calf and adult females–orphans on nonfed and fed pastures, respectively, which we later pooled together.

Data analysis

For both calves and females, a relative measure of body mass loss was estimated as the logarithm of the ratio between the body mass on March 16 (end of the experiment) and the body mass on January 7 (beginning of the experiment), hence a negative value reflects a somatic loss. The use of this metric was justified by the isometric relationship between log(mass in March) and log(mass in January) for females [on log-scale: $\beta=0.914$ (0.802, 1.027)], and for the calves [$\beta=0.872$ (0.702, 1.043)]. Because of missing March

Table 1 Composition of the two groups (fed versus nonfed) of animals used for the experiments; number of animals (*N*), mean age (years± standard error) (age±SE) of females and mean body mass (kg±standard error) (BM±SE) January 7; the start of the experiment

Site	Females						Calves			
	Calf at heel			Not calf at heel			Nonorphan		Orphan	
	<i>N</i>	Age±SE	BM±SE	<i>N</i>	Age±SE	BM±SE	<i>N</i>	BM±SE	<i>N</i>	BM±SE
Fed	12	5.3±0.6	84.3±1.7	8	5.9±0.7	85.8±2.1	12	49.6±1.2	6	52.7±1.0
Nonfed	12	5.5±0.6	82.6±1.7	8	5.0±0.7	83.3±2.1	12	49.3±1.1	6	49.2±1.0

weights of three calves (one died, one went missing and one not rounded up in March) and one female (not rounded up in March), these observations had to be omitted from the analyses. Females’ relative winter body mass change was used as a potential index of maternal post-weaning cost while calves’ relative winter body mass change was used as a potential index of post-weaning maternal care.

We used general linear model to test (1) the effect of “site” (nonfed versus fed; a measure of the effect of forage condition), calf sex and calves status (nonorphans versus orphans) on relative change in body mass of the calves, and (2) the effect of “site,” calf sex and post-weaning status (mother with calf at heel versus mother without calves at heel) on female relative change in body mass. The interactions between “site” and “calf status” as well as between “site” and “post-weaning status” were also tested, but were only considered if significant. A simple proportion test was performed to compare survival rate of fed versus unfed groups of calves and females.

We estimated the mean and standard error of the female–calves distance for each calves. From these values, we realised that one of the distance on the feeding site (on average, about 2,000 m) clearly appeared to be an outlier (this was a strayed animal who never join the group) and removed from the analysis. Using the distance data, we performed simple linear models to assess whether on average, the distances mother–calf and mother–orphans differed (1) between orphans and nonorphans in the fed and nonfed groups; and (2) as well as between fed and nonfed sites for orphans and nonorphans. All analyses were performed in SAS (2008) with a 95% significance level.

Results

Calves

The relative body mass loss of the orphaned calves was markedly higher than for calves following their mothers (Table 2a, Fig. 1). On an absolute scale (i.e., nontransformed), this represents a difference in body mass loss

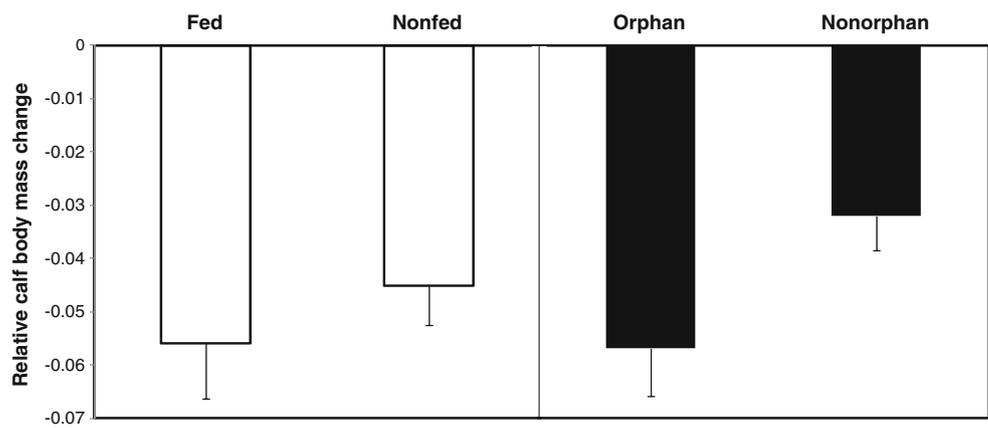
between orphans and nonorphans of 1.41 kg (SE=0.62). Nonfed versus fed calves’ lost equal amount of body mass (Table 2a, Fig. 1). The interaction term between the site and the calf status was not significant (Table 2a); however orphaned calves tended to lose somewhat more mass when there was increased interference competition (the fed group). Relative body mass loss did not differ between male and female calves (Table 2a). One of the nonorphaned calves in the fed group was found dead and one disappeared in February, giving a mortality rate of 0.08 for nonorphans, whereas no mortality was recorded among orphans. However, calf’s winter survival was not influenced by calf status even if both calves were entered as dead and the analysis was run separately for the fed group only (proportional test for difference: *P*=0.12).

Table 2 Parameter estimates and standard errors (SE) from the general linear models assessing the effect of the feeding regime [“Site”] (a measure of forage availability with two levels: nonfed and fed), calf status (with two levels: “Nonorphan” and “Orphan”), post-weaning status (a measure of reproductive cost with two levels: “With calf at heel” and “Without calf at heel”) and calf sex on (A) calves relative change in body mass and (B) females relative change in body mass

Dependent variables	Estimate	SE	<i>P</i>
A. Relative calf body mass loss (<i>R</i> ² =0.16; <i>N</i> =33)			
Intercept	-0.0299	0.010	0.006
“Site” (nonfed vs. fed)	0.0108	0.012	0.381
Calf status (nonorphan vs. orphan)	0.0277	0.013	0.040
Calf sex (male vs. female)	0.0046	0.013	0.723
Calf status × “site”	-0.0462	0.025	0.071
B. Relative female body mass loss (<i>R</i> ² =0.04; <i>N</i> =39)			
Intercept	-0.0118	0.011	0.305
“Site” (nonfed vs. fed)	0.0068	0.013	0.607
Females status (without calf vs. with calf)	0.0134	0.013	0.326
Calf sex (male vs. female)	-0.0032	0.014	0.818
Females status × “Site”	-0.0472	0.025	0.073

The variables “Site,” calf status, post-weaning status and calf sex were categorical with “fed,” “Orphan,” “With calf at heel” and “Female” respectively, used as reference levels. Results for the main effects are from model the interaction terms as they were not significant

Fig. 1 Relative body mass change [$\ln(\text{body mass March 16}/\text{body mass January 7})$]+SE in relation to the feeding regimes [(fed ($N=15$) and nonfed ($N=18$)] and the calf orphaning status [(orphaned ($N=12$) and nonorphaned($N=21$) calves)]



Females

Relative body mass loss did not differ between nonfed and fed females (Table 2b, Fig. 2), between females with and without calf at heel (Post-weaning status: Table 2b; Fig. 2) or depending on the sex of the calf at heel (Table 2b). The interaction term between the site and the post-weaning status was not significant (Table 2b); there was a tendency for females with calves at heel to lose somewhat more mass in the fed group. All females survived the winter.

Mother–calf and mother–orphan distances

There was a significant difference between mother–calf and mother–orphan distances both for the nonfed ($F_{1,7}=11.71, P=0.011$) and the fed ($F_{1,4}=8.90, P=0.041$) sites. Indeed, as expected, nonorphaned calves stayed closer to their mothers than orphans to females with calves at heel at both nonfed pasture (estimated difference in distance±SE= -39.94 ± 11.67 m, $t=-3.42, df=8, P=0.011$; Fig. 3) and fed sites (estimated difference in distance= -188.04 ± 63.05 m, $t=-2.98, df=5, P=0.041$; Fig. 3). Orphans were farther away from mothers in fed sites than in nonfed sites (mean±SE [fed: 203.89 ± 39 m; nonfed: 68.61 ± 34.5 m];

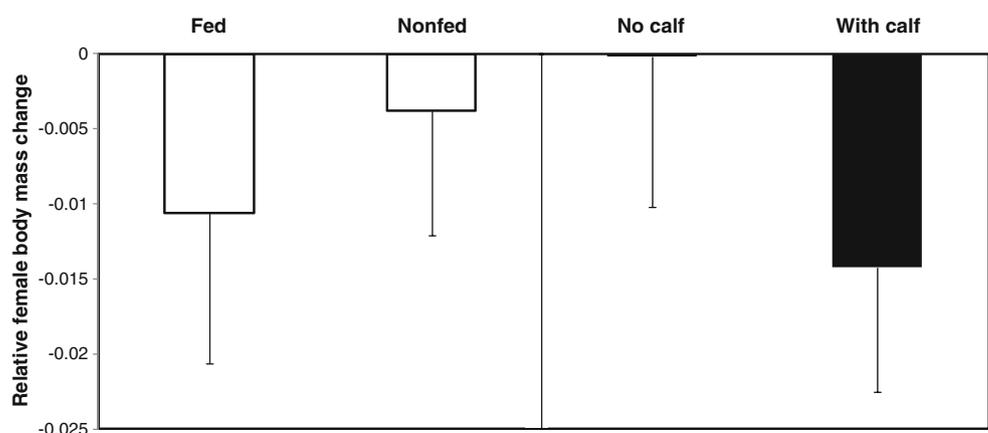
$t=2.57, df=6, P=0.05$), while there was no difference in distance among nonorphans ($F_{1,6}=0.85, P=0.39$).

Discussion

The most important component of maternal care in mammals, and the most costly one to the mother, is clearly lactation (Clutton-Brock et al. 1989). Due to this, studies of maternal care have been biased towards the period before weaning, despite the fact that most juvenile ungulates stay together with their mother during their first year of life even though being weaned (Lent 1974). The higher winter body mass losses among orphan compared to nonorphan reindeer calves provide rare evidence of post-weaning maternal care in ungulates. Body mass of calves are closely linked both to survival the first winter (Loison et al. 1999) and age at first reproduction (Langvatn et al. 2004). The mass losses reported here thus suggest demographic side effects of orphaning calves.

The lack of evidence of differences in survival is likely due to that our study was done during fairly favourable winter snow conditions, as confirmed by the mean snow depth for the 2 months in 2009 (26 cm) compared to the normal level (1961–1990) of 43 cm (meteorological station at Karasjok,

Fig. 2 Relative body mass change [$\ln(\text{body mass March 16}/\text{body mass January 7})$]+SE in relation to the feeding regimes [(fed ($N=19$) and nonfed ($N=20$)] and the reproductive status of the females [(females having calves at heel ($N=23$) or not ($N=16$)]



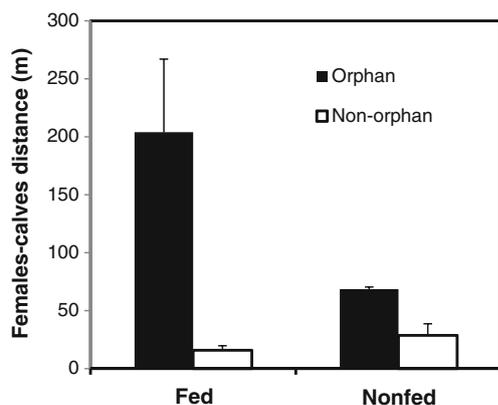


Fig. 3 Estimated mean distance (+SE) between offspring and their mothers and between those same females and the orphans at 12.00 every day of the month of February exposed to two feeding regimes (fed and nonfed). Sample sizes are five for nonfed-nonorphan, four for nonfed-orphan, three for fed-nonorphan and three for fed-orphan

Norway; <http://www.eklima.met.no>) and smaller overall somatic losses than usual. Mothers and their offspring (nonfed site) lost only 0.6 and 1.7 kg, respectively, during these 2 winter months (January 7– March 16, 2009) compared to around 4 and 6 kg, respectively, under normal winter conditions (Mika Tervonen, personal communication).

Benefits of mother–offspring bonding beyond lactation potentially include maternal protection against conspecifics and predators, transfer of knowledge from mothers to calves, such as learning the distribution of key habitats and resources, and where to seek cover. However, breaks in this transfer will probably be less eminent in flock living species as orphans are normally allowed to adhere to the herd (Lent 1974). In our case, the care seems to be manifested by protecting offspring from harassment and by sharing feeding resources, both craters (Barrette and Vandal 1986) as well as at feeding stations as indicated by the close mother–calf distance in both groups (Fig. 3). The more distant located orphans (Fig. 3) probably spend less time foraging as reported in low ranked peripheral distributed bison (*Bos bison*) (Berger and Cunningham 1988) and among several African ungulates (Underwood 1982). Indeed, having their mothers around may increase the calves' access to food and increase their effective forage time compared to orphans. Clutton-Brock et al. (1981) suggested that post-weaning maternal care in red deer was biased towards female calves in line with Kojola (1989) finding that winter body-mass losses in female reindeer calves were reduced with increasing females' rank in contrast to for male calves. However, we found no indication of sex-specific post-weaning care.

On lichen-poor range, the addition of supplementary fodder is likely to increase the level of interference competition and could thus be a further indicator of whether this is the critical aspect of post-weaning maternal care. Our

evidence was not fully conclusive, as there was only a trend ($P=0.07$) of higher relative losses among orphans in the group that was fed as compared to nonfed (Fig. 1). This may also be indicative of a negative effect of supplementary feeding (due to interference competition and harassment) on low-ranked individuals. Indeed, the orphans were partly kept away and spent less time at the troughs when food was available as compared to nonorphans (Mika Tervonen, personal communication). This was confirmed by their longer estimated mean distance to mothers with calves (~204 m, Fig. 3) at noon when supplementally fed as compared to ~69 m in the nonfed group. As on average, only around half of winter the animals' maintenance requirement was derived from supplementary food, this interference competition will be severe, although the daily string feeding practise reduces the overall competition. Also the competition around snow craters may increase as the animals normally scattered around the mobile feeding stations waiting for the daily ration. Staying in the outskirts of the herd will probably reduce the risk of losing craters to dominant herd members and ease the general harassment level. In contrast, the favourable snow conditions combined with the lichen rich range at the nonfed site eased the resource competition. Indeed, the orphans seem better able to crater without spending too much energy and to keep control, without too much interference, of the energy rich resource (i.e., lichens), even though their mean distance to adult females are much smaller (Fig. 3).

The lack of an effect of calves at heel on females' relative winter body mass change suggests that the maternal post-weaning cost is of minor importance in reindeer. This complies with Bårdsen et al.'s (2008) finding of a risk sensitive reproductive tactic in female reindeer to buffer against stochastic climatic winter conditions. Indeed, reindeer is classified as a capital breeder (Jönsson 1997). The short alpine and arctic summer demands early parturition relative to plant phenology (Reimers et al. 1983; Skogland 1989; Post 2003) and the females are drawing heavily on their own reserves during late gestation and first part of lactation (White and Luick 1984). They can therefore not afford to allocate heavily in their calves during winter. However, the favourable snow condition during the experiment and the general good females' January condition in the herd could mask differences in maternal reproductive costs as suggested by Kojola (1993).

Despite the widespread occurrence of orphaning, a by-product of autumn harvesting, little is known regarding consequences on offspring future fitness. Our study indicates that orphaning implies an extra mass loss during winter, which may incur survival costs in severe winters and reduce the phenotypical quality and increase age at maturation of females. Thus, there could be a demographic side effect of harvesting adult females.

Acknowledgements We thank the Finnish Reindeer Herders' Association and especially Mika Tervonen and his crew at the Kutuharju Experimental Reindeer Station for carrying out the experiment, and the Finnish Game and Fisheries Research Institute, at the Reindeer Research Station in Kaamanen, for logistic support. The study complied with the Finnish National Advisory Board on Research Ethics requirements.

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