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Lynx predation on semi-domestic reindeer: do age and sex matter?

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Abstract

The Eurasian lynx is an efficient stalking predator mainly selecting small-sized ungulates. In northern Scandinavia, semi-domestic reindeer are the only ungulate species available for Eurasian lynx year round and consequently constitute their main prey. Selective predation patterns by a predator on a domestic prey are likely to be influenced by husbandry practices and may have consequences for harvest strategies. We used data on 795 lynx-killed reindeer from northern Scandinavia collected in 2008–2011 to determine whether male and female Eurasian lynx preyed selectively on different age and sex classes of reindeer and how this was influenced by human-controlled seasonal changes in the composition of the reindeer herds. Lynx of both sexes were selected for reindeer calves year round although the proportions fluctuated seasonally, with peaks during summer and a drop after harvest. Male lynx switched to kill more adult reindeer in winter. There were no differences between the sexes of reindeer calves killed by lynx, but among adult reindeer male lynx selected for bulls over cows. We suggest that human-controlled seasonal variation in reindeer abundance is a main driver of prey selection by Eurasian lynx on semi-domestic reindeer.

Introduction

Prey selection by predators is influenced by the absolute and relative abundance of the prey species (Hebblewhite *et al.*, 2003; Cooley *et al.*, 2008), physiological characteristics (e.g. body size) of predators and prey (Sinclair, Mduma & Brashares, 2003; Owen-Smith & Mills, 2008), prey behaviour, and a diversity of environmental factors that may influence their accessibility (Gorini *et al.*, 2012). Preference for specific age classes of prey can strongly influence the demographic impact a predator has on the prey population (Sinclair *et al.*, 2003; Wilmers, Post & Hastings, 2007; Gervasi *et al.*, 2012). Predators that remove a significant proportion of adults, in particular prime age females, from a prey population will have a stronger impact than predators selecting mainly for juveniles and senescent individuals (Gaillard *et al.*, 2000; Wright *et al.*, 2006; Gervasi *et al.*, 2012). Non-selective stalking predators can potentially exert a stronger demographic effect than more selective coursing predators (Sinclair *et al.*, 2003), especially when they have a body size similar to that of the prey, and can kill prey across all age classes including prime age individuals. Most solitary felids prefer prey with a body mass less than or equal to their own weight (Jedrzejewski *et al.*, 1993; Hayward *et al.*, 2006; Hayward, Jedrzejewski & Jedrzewska, 2012).

In ungulates, vulnerability to predation depends on physical condition, size and maturity (Gorini *et al.*, 2012). Juveniles, individuals of old age and in poor condition (e.g. after or during reproductive investment or due to food limitation), are generally more exposed to predation than prime age individuals (Tveraa *et al.*, 2003; Molinari-Jobin *et al.*, 2004; Pole *et al.*, 2004; Knopff *et al.*, 2010). Physical traits in prey individuals, such as antlers, may be associated with increased risk for the predator when present and increased vulnerability for the prey during periods of absence (Clutton-Brock, 1982).

The effects of prey selection patterns in a predator–prey system involving wild prey may diverge from one with only livestock. Age and sex distribution in livestock herds are strongly regulated by human influence and are expected to display, due to slaughtering and breeding preferences, a higher seasonal variation in abundance of different age and sex classes during the year, with punctuated changes. Often when predators prey on livestock, they only constitute a part of their diet and general prey use depends on the abundance of the different wild and domestic prey species available (Meriggi & Lovari, 1996; Odden *et al.*, 2008; Mattioli *et al.*, 2011; Kamler, Klare & Macdonald, 2012; Vijayan, Morris & McLaren, 2012). Northern Scandinavia represents a system where semi-domestic reindeer are the only medium-sized

ungulate species occurring year round in significant numbers (Mattisson *et al.*, 2011b). Consequently, reindeer is the main prey in the diet of most carnivores in the region (Swenson & Andrén, 2005). The reindeer husbandry area covers about 40 and 50% of Sweden and Norway, respectively, where about 250 000 and 230 000 semi-domestic reindeer graze freely (largely unattended). The demographic structure in semi-domestic reindeer herds is highly skewed towards adult cows to permit maximum harvest yields, and a large proportion of the herds are harvested yearly (20–30%), with the offtake consisting mainly of calves [Reindeer Husbandry Administration (Norway); Sámi Parliament (Sweden)]. The Eurasian lynx *Lynx lynx* is widespread in the reindeer husbandry area and the inclusion of reindeer in lynx diet is substantial (70% in Mattisson *et al.*, 2011b; see also Haglund, 1966; Pedersen *et al.*, 1999). Lynx predation may have a large impact on reindeer husbandry with up to 15% estimated annual losses (Swenson & Andrén, 2005; Hobbs *et al.*, 2012). There is a legal requirement in Scandinavia that depredation should be fully compensated (Zabel & Holm-Müller, 2008; Mattisson *et al.*, 2011b); however, because of an extensive herding practices only a small proportion of the animals lost are actually verified as being killed by predators. Therefore, compensation payments are largely based on an estimation of the extent of predation. Increased knowledge on selection of killed reindeer is important to enable a compensation system that more accurately determines which losses are likely to be due to predation, and where possible compensate for actual impact on production rather than simple per capita losses. The age and sex selection of reindeer by lynx may also create consequences for the breeding strategies of the herders.

Here we study if lynx select certain age and sex classes of reindeer based on data from 795 kills made by 32 Global Positioning System (GPS)-marked lynx in northern Scandinavia. From the low body size ratio between lynx (F:17 kg, M:22 kg) and semi-domestic reindeer (F:65 kg, M:90 kg), we predicted a high proportion of calves in lynx diet, especially during summer when their abundance is high (before harvest), and that lynx preying on adult reindeer will select the smaller female reindeer (cows) over the larger males (bulls).

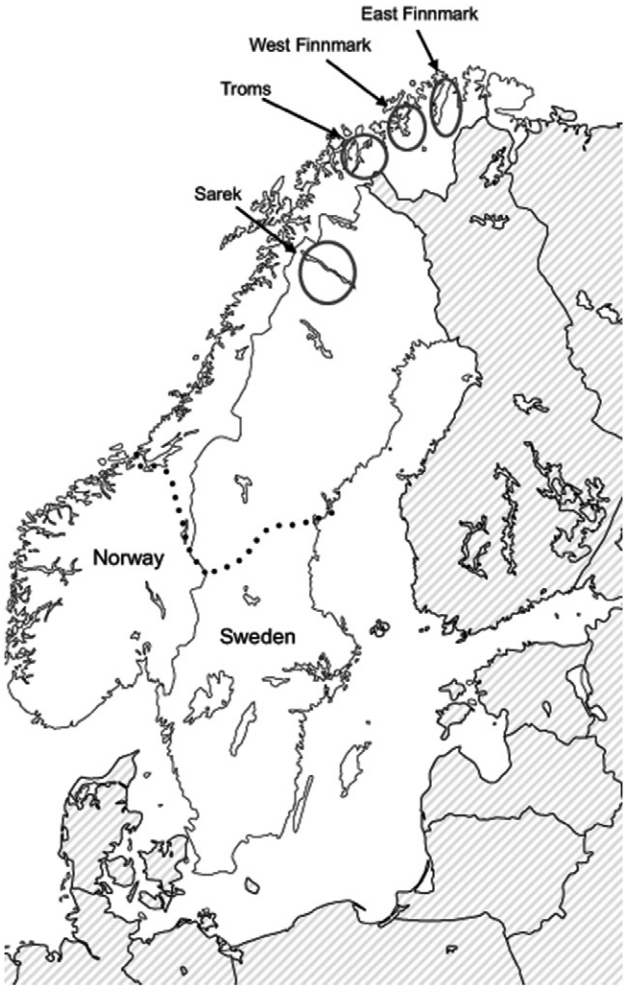

Figure 1 Map of Scandinavia (Sweden and Norway) showing the areas of data collection on reindeer killed by Eurasian lynx *Lynx lynx* in 2008–2011. The dotted line indicates the approximate southern border of the reindeer husbandry area in Norway and Sweden.

Materials and methods

Study areas

The study was conducted in Troms and Finnmark counties (69°00'–70°10'N, 19°90'–25°00'E) in Norway and in the Laponia ecosystem centred on Sarek National Park (67°00'N, 17°40'E) in Sweden (Fig. 1). Northern Norway is characterized by a coastal alpine climate. Alpine tundra dominates the area followed by mountain birch forest *Betula pubescens* and small patches of pine forest *Pinus sylvestris* along the coast and in some of the valleys. Sarek is characterized by a continental climate and the main vegetation is alpine tundra at higher elevations, sparse mountain birch forest in valleys and hillsides, and mixed conifer forest *Pin. sylvestris*, *Pic. abies* at lower elevations. All areas are usually snow covered from November to May.

Semi-domestic reindeer are managed exclusively and extensively by the indigenous Sámi people in the study area, and the ungulate community is dominated by semi-domestic reindeer across the study areas. The reindeer are moved seasonally between winter and summer ranges. Migration is a combination of natural seasonal movements and active herding-induced movements. Densities are generally high but with large spatial and temporal variation (Ims *et al.*, 2007; Tveraa *et al.*, 2007). Average regional densities in our study areas are 1–16 reindeers/km^2 (Mattisson *et al.*, 2011b). Free-ranging sheep are present during summer in the Norwegian part of the study area but only contribute to 7% of lynx diet (Mattisson *et al.*, 2011b). Moose *Alces alces* are the only wild ungulates occurring in significant numbers, but are not considered a prey for lynx because of its large size. Roe deer, the main prey of lynx in southern Scandinavia (Odden, Linnell & Andersen, 2006), are only found at extremely low densities in some few

Table 1 Reindeer killed by lynx *Lynx lynx* (*N* = 795) in northern Scandinavia between 2008 and 2010 separated by lynx sex and season

	Female lynx		Male lynx		
Reindeer category	Summer[a]	Winter[b]	Summer	Winter	Total
Calves (females)	2	9	5	9	25
Calves (males)	6	3	8	9	26
Calves (unknown sex)	144	44	148	19	355
Adult (cows)	13	16	16	27	72
Adult (bulls)	1	2	13	18	34
Adult (unknown sex)	85	18	57	11	171
Unknown age and sex		75		37	112

[a]1 May to 31 October.

[b]1 November to 30 April.

low-lying coastal areas and can therefore be regarded as functionally absent. Mountain hare *Lepus timidus*; tetraonids *Lagopus* spp., *Tetrao* spp.; red fox *Vulpes vulpes*; and small rodents *Clethrionomys* spp., *Microtus* spp. *and Lemmus lemmus* are alternative prey species for lynx (Mattisson *et al.*, 2011b).

Animal capture

Lynx were equipped with GPS collars after being darted from a helicopter and immobilized with medetomidine-ketamine, following pre-established protocols (Arnemo, Evans & Fahlman, 2011). We used GPS collars that either transferred data via the GSM network or with VHF/UHF data download in the field (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). The handling protocols were approved by the respective national ethics committees and wildlife management authorities.

Lynx-killed reindeer

Lynx-killed reindeer (Table 1, *n* = 795) were found during predation studies on 32 different lynx (18 adult females, 13 adult males and one 1-year-old male) in 2008–2011 by conducting field visits to clusters of GPS locations (see Mattisson *et al.*, 2011b for details). The age and sex of the reindeer were determined in the field whenever possible based on morphological criteria (body size, fur length and coloration, external genitals, antler size and shape). Scavenging is intense in parts of the area (Mattisson *et al.*, 2011a) occasionally resulting in few prey remains at the time of detection, such that age and sex were difficult to determine. We classified the reindeer as either calves (0–1 year), adults (>1 year) or of unknown age. The year was divided into summer (1 May to 31 October) and winter (1 November to 30 April). The summer period was chosen to completely include the pulse of availability of neonatal reindeer. A reindeer calf during summer was easy to separate from reindeer >1 year even when only part of the skin or hair was found because the colour and texture of the pelt are very different from adult reindeer. As a result, we did not have any reindeer of unknown age in summer. For winter, we excluded killed reindeer with unknown age from the analyses (*n* = 112). Small-sized summer calves may have been undetected during field visits because of few remains and total removal by scavengers, which may result in an underestimation of calves among lynx-killed reindeer. However, more than a fourth of the lynx kills found in summer were prey smaller than a reindeer calf (e.g. hare, ptarmigan; Mattisson *et al.*, 2011b), and the relatively long handling times even for calves (1.6 days in summer when calves are small compared with 2.6 days for adult reindeer; Odden *et al.*, 2010) suggest that the potential bias towards adult reindeer is rather low.

It was more difficult to determine sex than age of the reindeer, so sex was only known for 185 of the remaining 683 reindeer. We did not expect the likelihood of finding a killed reindeer with known sex to be skewed towards either sex (both sexes have antlers) or differentially effected by scavengers, and we concluded that analyses could still be performed even though a majority of kills were of unknown sex.

Reindeer population

The composition of winter herds after harvest (calves, adult bulls and cows) is reported annually on 31 March for each reindeer district, together with registered harvest data, to the responsible administration units for reindeer management (Reindeer Husbandry Administration: http://www.reindrift.no/?id=948&subid=0, 2007–2010; Sámi Parliament: http://www.sametinget.se/7284, 2007–2009). Each year between October and December, an average of 20–30% of the herd is harvested with the majority of the harvested reindeer being calves (~70%). Based on the reindeer districts in which the lynx-killed reindeer were found (*n* = 19), the reported proportions of calves were 9–33% after harvest. Among reindeer >1 year, the proportion of cows were 77–96% and bulls 4–23%. However, the accuracy of these numbers varies among districts and years (Fauchald *et al.*, 2004; Herfindal *et al.*, 2011). Summer distributions were not available, but even though the proportion of cows having calves vary among years and districts and depend on the age structure among females (Helle & Kojola, 1993; Tveraa *et al.*, 2003, 2007), the proportion of calves in summer can never exceed 49% (96% cows in winter herd, each getting one calf gives a theoretical maximum of 49% calves in summer herd). A 1:1 sex ratio in newborn calves is expected (Kojola & Eloranta, 1989), but this ratio will be skewed towards females after harvest because slaughter is strongly biased towards male calves.

Statistical analysis

We used chi-square tests to analyse differences in the distribution of age (calf, adult) or sex of reindeer (F, M) between seasons (summer, winter) and sex of lynx (F, M).

To reduce possible bias (due to low accuracy in the data) when analysing selection of reindeer killed by lynx, we avoided directly using the reported composition in the comparisons. Instead, we compared the 95% confidence intervals (CIs) for the proportions among the kills with the range of reported age and sex distributions of the semi-domestic reindeer populations in winter. If there is an overlap between the 95%

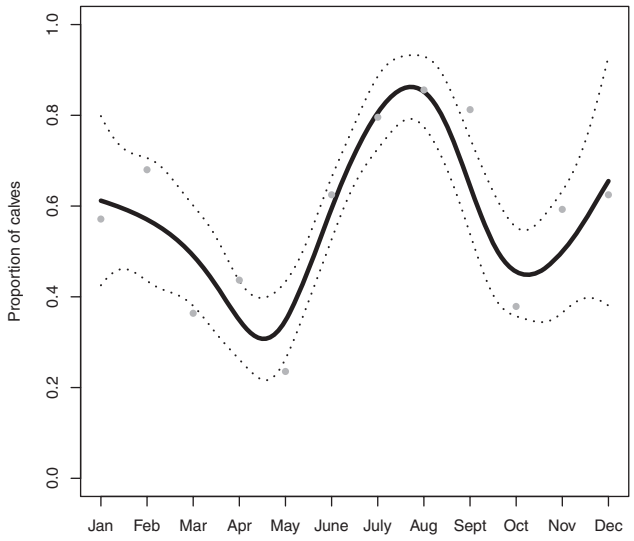

Figure 2 Yearly distribution of the proportion of calves among reindeer killed by lynx *Lynx lynx* in Scandinavia in 2008–2011. Dots represent the summarized proportions per calendar month, and a generalized additive model (GAM) with cubic regression spline was used to fit the smoothing curve, here shown with two standard error bands. The optimal amount of smoothing was estimated using a cross-validation.

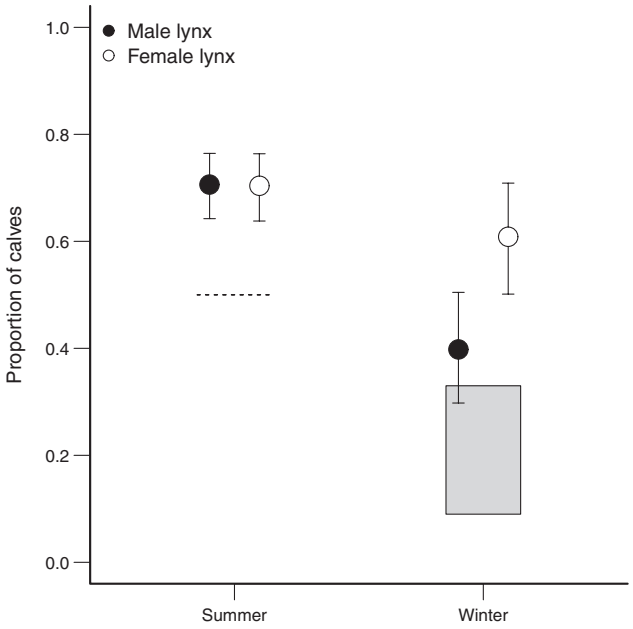

Figure 3 Proportion of calves among reindeer killed by lynx *Lynx lynx* in northern Scandinavia in 2008–2011 separated by lynx sex and season. The grey polygon represents the range of reported calf proportions in winter herds among the relevant reindeer districts, the striped line shows the maximum proportion of calves in summer herds, and error bars are Clopper–Pearson 95% confidence intervals (CIs). A lower CI above the reported range implies selection for calves by the lynx.

CI and the reported or estimated proportion, then there is neither selection nor avoidance.

Results

Calves composed a higher proportion of all lynx-killed reindeer in summer (62%; see Table 1 for all sample sizes) compared with winter (50%, $\chi^2 = 8.3$, d.f. = 1, $P = 0.004$) with a peak in July–September (Fig. 2). Overall, the proportion of calves among killed reindeer did not differ between female and male lynx ($\chi^2 = 0.3$, d.f. = 1, $P = 0.57$). However, when analysing the summer and winter seasons separately, male lynx killed a lower proportion of calves (40%) than female lynx (60%) in winter (Fig. 3; $\chi^2 = 7.4$, d.f. = 1, $P = 0.007$), while there was no difference between the sexes in summer (Fig. 3; $\chi^2 = 0.95$, d.f. = 1, $P = 0.33$). The lower limit of the 95% CI for the proportion of calves among lynx-killed reindeer in summer was higher than the theoretical maximum proportion of calves in the population (49%) for both female and male lynx (Fig. 3). In winter, the 95% CI for female lynx was well above the highest proportion of calves reported from all reindeer districts in the study area (33%), while the lower CI for male lynx slightly overlapped with the upper range (Fig. 3). This suggests that lynx in our study area actively selected reindeer calves in both seasons in most areas.

Considering only adult reindeer (≥1 year), female lynx killed a much lower proportion of bulls (9%) than male lynx did (42%; Fig. 4, $\chi^2 = 9.4$, d.f. = 1, $P = 0.002$). The lower 95% CI for bulls killed by male lynx was above the range of reported proportions of bulls (4–23%) in the standing populations, while the 95% CI of bulls killed by female lynx overlapped the reported range (Fig. 4). This suggests that male lynx selected for bulls, whereas female lynx did not select for any sex. The sex ratio of killed calves did not differ between male and female lynx (Fig. 4; $\chi^2 = 1.6$, d.f. = 1, $P = 0.69$), and after pooling male and female lynx the sex ratio of reindeer calves killed by lynx did not differ from the expected 1:1 sex ratio ($\chi^2 = 0.02$, d.f. = 1, $P = 0.89$).

Discussion

Lynx predation patterns on semi-domestic reindeer differed seasonally and with respect to sex and age of both predator and prey, further influenced by seasonal human-controlled variation in reindeer herd composition, especially in the availability of calves. While a selection for calves was detected, lynx still killed a large proportion of adults more than twice their own size. The magnitude of the actual losses of reindeer to predators as well as the design of the compensation system (Zabel & Holm-Müller, 2008; Næss *et al.*, 2011) is hotly debated in Scandinavia. Knowledge of selection for sex and age is a prerequisite to address the demographic effect of lynx on semi-domesticated reindeer, with consequences for both harvest strategies and the compensation system.

Felids generally attempt to minimize risks associated with predation by targeting easier prey (Owen-Smith & Mills, 2008;

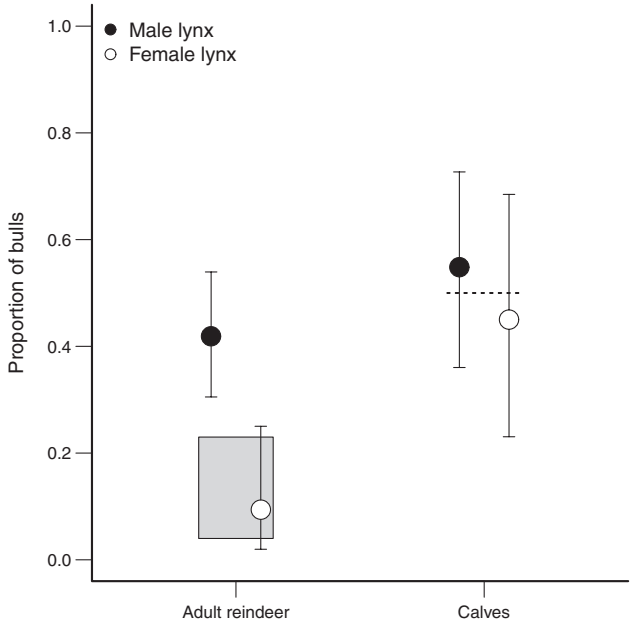

Figure 4 Proportion of bulls among reindeer killed by lynx *Lynx lynx* in northern Scandinavia in 2008–2011 separated by male and female lynx and the age of reindeer. The grey polygon represents the range of reported bull proportions (adults only) in winter herd among relevant reindeer districts, the striped line shows the expected proportion of males among newborn calves, and error bars are Clopper–Pearson 95% confidence intervals (CIs). A lower CI above the reported range implies selection for bulls/male calves by the lynx.

Knopff *et al.*, 2010). Each prey category requires not only a different effort to kill, but also represents a different gain in terms of food biomass. A predator is expected to select for the most profitable prey considering encounter rate, hunting success and risk of injuries (Mattioli *et al.*, 2011). Eurasian lynx are distributed across large parts of Scandinavia, and outside the reindeer husbandry area they mainly prey on roe deer (Odden *et al.*, 2006). The body size of adult roe deer (20–25 kg) and lynx is rather similar, and lynx do not select for roe deer calves (Okarma *et al.*, 1997; Molinari-Jobin *et al.*, 2002; Mejlgaard *et al.*, 2013). In contrast, we demonstrate that lynx preying on the much larger reindeer did select for calves year round, a pattern previously observed also for the larger red deer *Cervus elaphus* (Okarma *et al.*, 1997). Still, almost half of the killed reindeer were older than 1 year, suggesting that the risk involved in preying on adults may be lower than expected based on the body size of reindeer, possibly an effect of the semi-domestic nature of the reindeer. This is further supported by the short time lynx spend on each reindeer kill site (~2 days; Odden *et al.*, 2010) relative to the size of the prey, and leads us to reject the presumption that lynx would kill larger animals to gain more biomass per unit of hunting effort (cf. Mattson, 2007). Considering a daily food requirement of ~1.7 kg for lynx (Andrén *et al.*, 2011), even a winter calf (~40 kg) should be sufficient for several days of feeding.

Calf predation peaked in July and August when calves are still small and highly vulnerable. The sudden drop in proportion of calves killed in October coincides with the start of the annual harvest of reindeer (October–January). The proportion of calves harvested are very high (~70%), likely decreasing the relative availability of calves for the lynx.

The proportion of bulls among adult reindeer in the male lynx diet were higher than expected from availability, suggesting selection for reindeer bulls even though bulls are four times the size of a male lynx. If caused by exhaustion from rutting activities, bulls should be preferred from the end of the rutting season in October/November until the onset of new plant growth next spring (cf. Pole *et al.*, 2004; Knopff *et al.*, 2010). However, no bulls were found killed by lynx after or during the rutting season (all were killed between January and July; Supporting Information Table S1), suggesting other causes for the selection (Molinari-Jobin *et al.*, 2004). Reindeer bulls lose their antlers in November–December while cows retain theirs until early summer after the calves are born. It could be speculated that lynx avoid attacking prey with protective antlers due to the risk of injures as the absence of confirmed lynx-killed bulls coincided with the time when bulls have shed the velvet from their antlers and have the most efficient weaponry. Cows were preyed upon more or less year round regardless of where they were in their antler cycle, indicating that the smaller female antlers may not be sufficient to deter the lynx. An alternative explanation could be that the observed selection for bulls by male lynx was not an active choice but more a reflection of an increased encounter rate with bulls at some spatio-temporal scales (Gorini *et al.*, 2012). During calving, cows are drawn to higher grounds (Mårell & Edenius, 2006) mainly as an anti-predator strategy against forest-dwelling predators, while bulls gather in small groups below the treeline, selecting for the best forage. Lynx in mountainous areas of northern Scandinavia select for the birch forest band just below the treeline (Rauset *et al.*, 2013), which may increase the likelihood of encountering a bull over a cow during parts of the year even though cows are generally more abundant. However, as we have no data on habitat use or sexual segregation in reindeer, this remains a speculation.

Consequences of intensive lynx predation in this predator-livestock system (Mattisson *et al.*, 2011b) may influence both the harvest strategies of the reindeer herders and the demography and dynamics of the prey population. High losses of adult reindeer may impair the reindeer herders' ability to freely select for the best breeding individuals (simply by reducing the number they can select from), which can result in a tendency to build larger herds to buffer against uncertainties (Næss *et al.*, 2011). On the other hand, high losses of calves may reduce the annual offtake as the harvest target calves. Although we observed a selection for reindeer calves by lynx, the proportion of adults among the killed reindeer were still substantial (even if considering a possible overestimation of adults due to a higher probability of failing to find killed calves), accentuating the potential ability of lynx to affect reindeer population growth (Gervasi *et al.*, 2012). However, lynx predation on semi-domestic reindeer may be, at least partly, compensatory to other sources of mortality. Large

herd sizes resulting in food limitation during harsh winters can result in increased mortality in reindeer (Tveraa *et al.*, 2007), and poor condition in reindeer cows increases predation rates on calves (Tveraa *et al.*, 2003). A compensatory relationship between mortality due to food limitation and predation can thus reduce the impact of predation on reindeer demography and population dynamics in areas with low productivity (Tveraa *et al.*, 2003, 2007) and in large herds with strong intraspecific competition. Hobbs *et al.* (2012) demonstrated that a combined effect of increased abundance of lynx, negative density dependence, latitude and unfavourable weather conditions decreased reindeer harvest in Sweden by reducing population growth. Thus, the impact of lynx predation on reindeer demography is likely shaped by both intrinsic and extrinsic factors which can be expected to vary between years, regions and countries.

We conclude that age and sex category of both predator and prey affected the selection patterns in our study. In addition, lynx selection for the different reindeer categories differed between seasons, probably determined by human harvest strategies. The seasonal selection rates reported here could be incorporated into compensation payment systems (Zabel & Holm-Müller, 2008; Mattisson *et al.*, 2011b; Næss *et al.*, 2011). A compensation system based on accurate predictions, reflecting the actual impact of predation, will hopefully lead to a reduction in conflict level and increase acceptance for carnivores. Research that enhances the understanding of predator–livestock interactions is thus important for the management of large carnivores especially in areas of high conflict.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Reindeer killed by lynx ($N = 795$) in northern Scandinavia between 2008 and 2010 separated by month of the year and category of reindeer.