



## Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system?

Jenny Mattisson<sup>a,b,\*</sup>, John Odden<sup>b</sup>, Erlend B. Nilsen<sup>b</sup>, John D.C. Linnell<sup>b</sup>, Jens Persson<sup>a</sup>, Henrik Andrén<sup>a</sup>

<sup>a</sup> Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden

<sup>b</sup> Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

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### ABSTRACT

Semi-domestic reindeer (*Rangifer tarandus*) are the main prey for lynx (*Lynx lynx*) in northern Scandinavia. This causes large, but poorly documented, losses of reindeer. Although the compensation schemes differ between Norway and Sweden, there is a legal requirement in both Scandinavian countries that losses of semi-domestic reindeer to large carnivores should be fully compensated. The current level of compensation payment is based on limited data on lynx kill rates on reindeer. The main goal of this study was to quantify lynx kill rates on reindeer across a range of ecological conditions in northern Scandinavia. A total of 35 lynx were monitored during 3667 days. All lynx individuals killed reindeer. However, we observed a high variation in individual kill rates. Kill rates were strongly affected by sex and social status (i.e. females with and without kittens), as well as season and reindeer availability. The highest kill rates were observed in summer for male lynx, and the lowest were observed during winter for solitary lynx at low reindeer density. In summer, several female lynx switched completely to small prey species even at high densities of reindeer. The present political goals for lynx conservation in Scandinavia require that lynx occur in the reindeer husbandry area where reindeer are the only suitable ungulate prey available. Accordingly, it is therefore impossible to have the total prevention of depredation as a management goal. Rather depredation levels must be limited such that they are considered acceptable, and fair compensation payments should be paid. Our study is the first empirical quantification of the magnitude of lynx depredation on semi-domestic reindeer. This is an important step necessary to enable the setting of fair compensation levels and will hopefully lead to a reduction in conflict level concerning the potential impacts that lynx have on reindeer.

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### 1. Introduction

Livestock depredation by large carnivores is one of the most common causes of human-wildlife conflicts (Thirgood et al., 2005). Livestock depredation is often unevenly distributed in space and time and can have a significant socio-economic impact on individual farmers or herders where it occurs (Thirgood et al., 2005; Zimmermann et al., 2010). Many large carnivore species are now recovering and expanding into new areas (Landa et al., 2000; Linnell et al., 2009), resulting in a growing concern from livestock owners. In Scandinavia (Sweden and Norway), the Eurasian lynx (*Lynx lynx*) population increased rapidly in the mid 1990s resulting

in increased depredation and conflicts with semi-domestic reindeer (*Rangifer tarandus*) and sheep (*Ovis aries*) herders (Swenson and Andrén, 2005; Linnell et al., 2010). In Scandinavia, reindeer are managed almost exclusively by indigenous Sámi people and husbandry is typically extensive. Norway has signed the International Labour Organization (ILO) convention on Indigenous and Tribal Peoples in Independent Countries, and both Sweden and Norway have signed the UN's International Covenant on Civil and Political Rights and are thereby committed to sustain the Sámi culture in which reindeer management is an important part. Likewise both countries are signatories of the Council of Europe's Bern Convention on the Conservation of European Wildlife and Natural Habitats, and Sweden is bound by the European Union's Habitats Directive (Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora). Consequently, management needs to find compromises between the conservation of carnivores and the sustainability of reindeer husbandry (Nilsson Dahlström, 2003). The reindeer husbandry area covers ~50% of

\* Corresponding author at: Norwegian Institute for Nature Research, 7485 Trondheim, Norway. Tel.: +47 73801400; fax: +47 73801401.

E-mail addresses: [jenny.mattisson@nina.no](mailto:jenny.mattisson@nina.no) (J. Mattisson), [john.odden@nina.no](mailto:john.odden@nina.no) (J. Odden), [erlend.nilsen@nina.no](mailto:erlend.nilsen@nina.no) (E.B. Nilsen), [john.linnell@nina.no](mailto:john.linnell@nina.no) (J.D.C. Linnell), [jens.persson@slu.se](mailto:jens.persson@slu.se) (J. Persson), [henrik.andren@slu.se](mailto:henrik.andren@slu.se) (H. Andrén).

Sweden and ~40% of Norway, where 250,000 and 230,000 reindeer, respectively, graze freely, mainly unattended (Anonymous, 2010, 2011). The natural seasonal migration of reindeer between winter and summer pastures is largely maintained, but is increasingly governed by the owners and land use restrictions. Both countries experience extensive depredation on semi-domestic reindeer mainly by lynx and wolverine (*Gulo gulo*), but also by brown bear (*Ursus arctos*), golden eagle (*Aquila chrysaetos*) and to some degree grey wolf (*Canis lupus*; Bjärvall et al., 1990; Nybakk et al., 1999; Sikku and Torp, 2004; Swenson and Andrén, 2005).

In Scandinavia, there is a legal requirement that depredation losses of semi-domestic reindeer should be fully compensated, and the subsequent cost of compensation for large carnivores in 2010 was US\$ 8.5 million and US\$ 10.4 million in Sweden and Norway, respectively, where lynx were held responsible for ~40% of the total compensation (Swedish Environmental Protection Agency, The Norwegian Directorate for Nature Management). However, the compensation schemes differ between the countries. In Norway, ex post facto compensation (Schwerdtner and Gruber, 2007) is based on an estimation of losses and is paid directly to the owners. However, the detection rate of carnivore-killed reindeer is very low (9% in winter and 2% in summer; Odden, J., Personal communication) so there is a high degree of uncertainty concerning the real magnitude of depredation. In Sweden, the compensation scheme is based on the presence and density of carnivores and a risk-based compensation (or compensation in advance according to Schwerdtner and Gruber, 2007) is paid to each of the 51 reindeer grazing cooperatives (Zabel and Holm-Müller, 2008). When compensation is based on the presence of carnivores rather than actual losses, reliable estimates of carnivore density (Andrén et al., 2002; Linnell et al., 2007) and individual kill rates are essential. Still, the current level of compensation is based on uncertain and limited information concerning kill rates. The lynx-reindeer conflict is unique in the sense that semi-domestic reindeer are the only suitable ungulate prey species available for the lynx throughout most of the reindeer husbandry area (Andersen et al., 1998 and chapters therein) and consequently, as lynx are largely specialized on medium-sized ungulates (Pedersen et al., 1999; Odden et al., 2006; Molinari-Jobin et al., 2007), reindeer are the main prey.

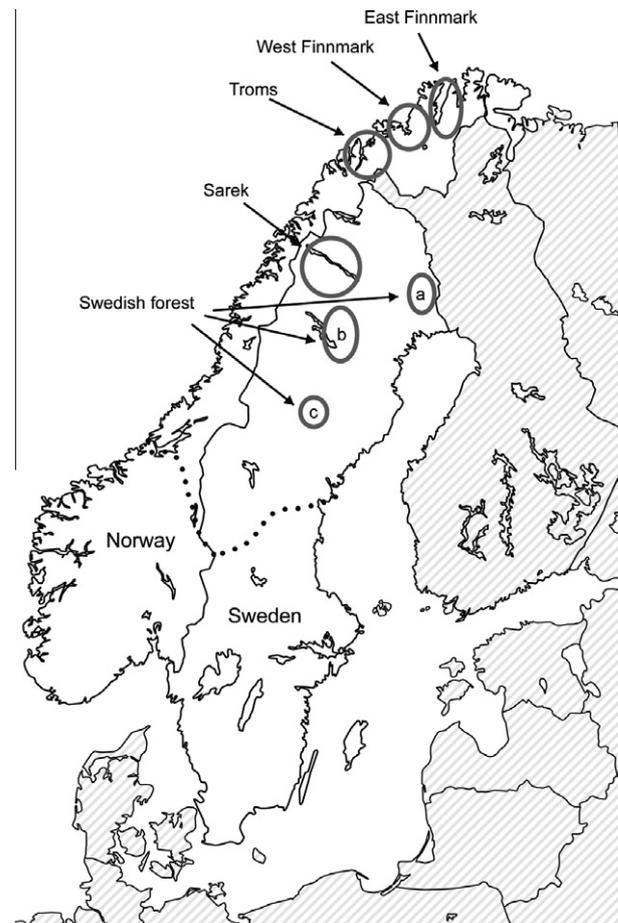
The fact that lynx prey on reindeer is well documented (Haglund, 1966; Bjärvall et al., 1990; Nybakk et al., 2002) but the only existing data on individual kill rates on reindeer are limited to a few studies of family groups in a few winters (Pedersen et al., 1999; Sunde et al., 2000). In contrast, lynx kill rates on roe deer (*Capreolus capreolus*) and domestic sheep have been extensively studied throughout Europe, and are known to vary depending on sex and demographic status, individual preferences, prey density, prey composition and areas (Sunde and Kvam, 1997; Okarma et al., 1997; Sunde et al., 2000; Molinari-Jobin et al., 2002; Odden et al., 2002, 2006; Nilsen et al., 2009). An understanding of ecological factors causing variation in kill rates will be essential in order to reach a fair compensation scheme. The aim of this study was to fill this gap by quantifying lynx kill rates on reindeer across a range of ecological conditions, focusing in particular on the effects of lynx sex or social status, season, and reindeer availability. These results will then be interpreted in the context of the knowledge needs that exist for Scandinavian compensation schemes to be fair.

## 2. Study areas

The study was conducted in northern Scandinavia, over a series of areas scattered across the northern parts of Norway and Sweden (Fig. 1). The most intensive studied areas were in Troms (69°00'N, 19°90'E), western Finnmark (70°00'N, 23°30'E), and eastern Finn-

mark 70°10'N, 25°00'E) in Norway, and Sarek (67°00'N, 17°40'E) in Sweden. 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 (Oksanen and Virtanen, 1995). 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 (*P. sylvestris*, *Picea abies*) at lower elevation. In addition, we monitored some lynx outside the main study areas, hereafter called Swedish forest sites: Tornedalen (66°30'N, 22°80'E), Arvidsjaur (66°20'N, 18°00'E) and Vilhelmina (64°30'N, 16°60'E). These areas are dominated by mixed conifer forest interspersed with bogs and wetlands. All areas are usually snow-covered from November to May.

The ungulate community is dominated by semi-domestic reindeer in all areas. Reindeer are not evenly spread over the grazing areas, are normally seasonally migratory, and are highly mobile within seasons, resulting in large spatial and temporal variations in densities. However, when averaging densities (total counts of reindeer in winter herds per grazing cooperative in 2008/2009) across the administrative areas used by radio-collared lynx, reindeer densities were in the region of 1–16/km<sup>2</sup> inside our study areas (based on official statistics from the Reindeer Husbandry Administration in Norway: <http://www.reindrift.no/?id=948&subid=0>, and the Sámi Parliament in Sweden). In Norway, free ranging sheep are present in most areas during summer. Moose (*Alces alces*) are the only wild ungulate occurring in significant numbers throughout



**Fig. 1.** Map of Scandinavia (Sweden and Norway) showing the areas of data collection on lynx (*Lynx lynx*) predation on reindeer. The dotted line indicates the southern border of the reindeer husbandry area in Norway and Sweden. Swedish forest is represented by Tornedalen (a), Arvidsjaur (b) and Vilhelmina (c).

the study areas, but some roe deer exist sporadically in low altitude or coastal areas. Mountain hare (*Lepus timidus*), tetranoids (*Lagopus lagopus*, *Lagopus muta*, *Tetrao urogallus*, *Tetrao tetrix*), red fox (*Vulpes vulpes*), and small rodents (*Clethrionomys* spp., *Microtus* spp. and *Lemmus lemmus*) are potential alternative prey species for lynx in all the areas.

### 3. Methods

#### 3.1. Animal capture

Lynx were equipped with GPS-collars after being darted from a helicopter and immobilized with medetomidine–ketamine, following pre-established protocols (Arnemo et al., 2011). In Sweden, we used store-onboard GPS-collars (Televilt Posrec™ C300, TVP positioning AB, Lindesberg, Sweden) in 2002–2007 and GPS-collars with either GSM communication or UHF communication with VHF data download (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany) in 2008–2010. In Norway, Televilt GSM/GPS collars (Tellus™ 3H2A) were used in 2007 and Vectronic GSM/GPS-collars were used in 2008–2010. Individuals in Sarek were additionally equipped with intraperitoneally implanted VHF-transmitters (IMP/400/L, Telonics Inc., Mesa, AZ, USA) for long term monitoring. When possible, lynx were recaptured and the collar replaced when the battery was depleted. The handling protocol has been approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee and fulfils their ethical requirements for research on wild animals. In addition, permits for wild animal capture were obtained from the Swedish Environmental Protection Agency and the Norwegian Directorate for Nature Management.

#### 3.2. Lynx kill rate

We conducted predation studies on 48 different lynx between 2002 and 2010, of which we obtained high-quality kill rate data from 35 individuals (24 females, 11 males) during 128 periods of intensive tracking yielding estimates of kill rates between 2005 and 2010. Data on lynx kill rate on reindeer were obtained by identifying potential predation sites from GPS-location data (Sand et al., 2005; Knopff et al., 2009). During this study, the technology and battery life of GPS-collars greatly improved allowing for a higher location frequency and longer monitoring periods. This resulted in a high variation of these variables between kill rate periods, depending on the collar type used and the possibilities of re-collaring the lynx following battery depletion (Table S1). Because of the variation in location frequency between kill rate periods, we identified clusters visually using GIS-software (ArcView 3.3 and ArcMap 9.3, ESRI) and a web-based map-system for displaying telemetry data (<http://www.dyreposisjon.no>). The number of locations required to define a cluster, later visited in the field, was based on at least two locations within 100 m. We attempted to visit all clusters and even several single locations; however, the logistical difficulty in accessing portions of our study area required a priority assessment. As our knowledge of the animals' behaviour increased during the study period, less priority was given to clusters that were assumed to be daybeds (i.e. a series of day time locations within a very limited area, without revisits, often in steep terrain) while all sites that were revisited by the lynx (i.e. two non-continuous GPS-locations within 100 m) or where the lynx stayed  $\geq 1$  night (see Nilsen et al., 2009 for details) were given highest priority. In addition, single locations around clusters were visited when logistically possible. We visited 2189 clusters during 3667 monitored lynx days, i.e. on average 0.6 ( $\pm 0.34$  SD) clusters per monitored lynx day. We visited many clusters that had no prey

**Table 1**

Prey found at clusters from Eurasian lynx (*Lynx lynx*) in Northern Scandinavia, 2002–2010, grouped by season and reindeer density (high = reindeer grazing areas within lynx home range during the kill rate period; low = no reindeer grazing areas within lynx home range). Percentages are based on frequency of occurrence.

Prey species	Summer high n (%)	Winter high n (%)	Winter low n (%)	All year n (%)
Reindeer ( <i>Rangifer tarandus</i> )	255 (62)	342 (86)	14 (15)	1008 (70)
Sheep ( <i>Ovis aries</i> )	29 (7)	5 (1)	2 (2)	66 (5)
Roe deer ( <i>Capreolus capreolus</i> )		1 (0.3)		2 (0.1)
Moose ( <i>Alces alces</i> ) <sup>a</sup>	1 (0.2)			1 (0.07)
Mountain hare ( <i>Lepus timidus</i> )	73 (18)	28 (7)	31 (34)	202 (14)
Red fox ( <i>Vulpes vulpes</i> )	7 (1)	2 (1)	22 (24)	49 (3)
Domestic cat ( <i>Felis catus</i> )			7 (8)	9 (0.6)
Other mammals <sup>b</sup>	5 (1)	1 (1)	4 (4)	9 (1)
Ptarmigan ( <i>Lagopus</i> sp.)	17 (4)	7 (2)	5 (5)	39 (3)
Capercaillie ( <i>Tetrao urogallus</i> )	11 (3)	6 (2)		24 (2)
Black grouse ( <i>Tetrao tetrix</i> )	2 (0.5)	1 (0.3)	1 (1)	7 (0.5)
Other birds <sup>c</sup>	8 (2)	2 (0.5)	2 (2)	19 (1)
Scavenging events <sup>d</sup>	1 (0.2)	2 (0.5)	3 (3)	6 (0.4)
Kleptoparasitism <sup>e</sup>				2 (0.1)
Total prey	409	397	91	1443
Lynx individuals	28	28	10	48
Cluster visited	964	1004	221	>3700
Monitoring days	1533	1691	443	

Note: All year includes additional prey and cluster collected in 2002–2010, not included in the analyses.

<sup>a</sup> Calf killed July 2.

<sup>b</sup> Red squirrel (*Sciurus vulgaris*), European otter (*Lutra lutra*), stoat (*Mustela erminea*).

<sup>c</sup> Common teal (*Anas crecca*), bean goose (*Anser fabalis*), carrion crow (*Corvus corone*), gulls (*Laridae* sp.), Eurasian woodcock (*Scolopax rusticola*), bohemian waxwing (*Bombicilla garrulus*), fieldfare (*Turdus pilaris*), hazel grouse (*Bonasa bonasia*).

<sup>d</sup> Two moose, two reindeer, one harbour porpoise (*Phocoena phocoena*), one bait station for fox hunting.

<sup>e</sup> Salmon (*Salmo salar*) kleptoparasitised from otter in winter.

remains (61%) and several with small prey (12%; i.e. non-ungulate species <10 kg, Table 1), thus we are confident that we found the majority of killed reindeer. Still, we have almost certainly underestimated the number of small prey as they are more difficult to find, may not persist long, and may be so small that no clusters are formed when they are killed and completely consumed. Because of the store onboard collars (until 2007) and difficult weather conditions (mostly in winter and spring, e.g. avalanche risk, flooded rivers), the time elapsed between the locations of the lynx and the field visits ranged from 1 to 243 days. From 2007 and onward >80% of the clusters were visited within 1 month. However, the detection rate for finding prey remains did not decrease with time elapsed (logistic regression: wald test  $z = 0.00$ ,  $df = 1$ ,  $p = 0.99$ ); based on a subset of the data (657 clusters: 1–227 days, mean = 29 days, SE = 1.28). Because the study areas are located at high latitudes ( $\sim 70^\circ\text{N}$ ) with a cold climate, hair and bones from killed prey remain long after the time of death.

Reindeer carcasses found at clusters were defined as probably lynx-killed when we found prey remains (e.g. hair, rumen, bones) that matched the date of the cluster and where there were no other signs of cause of death. Confirmed lynx-kills were defined by clean bite marks to the throat of a reindeer. Lynx rarely scavenge (0%: Pedersen et al., 1999; 2%: Odden et al., 2006) and we only assigned scavenging to carcasses that clearly had been killed by something other than the lynx or if the estimated carcass age differed from the dates of the cluster. If a lynx revisited its own kill weeks after the time of death it was not defined as scavenging as such cases represent a return to a previous killed prey. Reindeer carcasses found at single locations were only assigned to that lynx if there were bite marks to the throat or other circumstances linked the monitored lynx to the kill. A kill event was classified as a multiple kill when more than one reindeer was killed by the lynx within a 500 m radii

and the GPS-locations indicated that they were killed during the same event (but not if killed during a return trip to a previous kill).

Sex and social status of the lynx: solitary independent females, family groups (adult females with kittens), or independent males, was assigned to each kill rate period as well as, season: winter (October–April) or summer (May–September), and low or high reindeer density (Table S2). Natal lairs of female lynx were visited in June–July to confirm reproduction, and survival of the kittens was monitored during the following autumn/winter by snow-tracking. Kittens usually leave their mother in March–April the next year (~10 months of age; Samelius et al., in press). Females with kill rate periods in April and May were assumed to be alone if no clear observations (visually or through tracks in snow) indicated differently. The summer period was chosen to completely include the birth pulse of neonatal reindeer. We used “low” and “high” reindeer density instead of continuous reindeer density because of the patchy distribution of reindeer and the lack of availability of data with a suitably fine-scaled spatio-temporal precision, making it impossible to estimate their functional density from a lynx’s point of view during a given kill rate period. High density indicates seasonal or year-round grazing areas (i.e. reindeer herds are allowed to stay year around) within the lynx home range at the time of the kill rate period while low density indicates an absence of seasonal grazing areas. Low density represents none, or just a few stray reindeer remaining after seasonal migration, while high density can vary from scattered herds with few reindeer in year round grazing areas up to very high densities on seasonal grazing areas. Spatial data describing reindeer grazing areas was obtained from GIS-layers compiled by the reindeer husbandry administration of Norway (<https://kart.reindrift.no/reinkart/>) and the County administrations in Sweden (GIS data Länsstyrelserna© 2000–2008, SWECO) and approximate dates for reindeer arrival or departure from seasonal ranges were obtained from local informants. In the winters of 2008–2009 and 2009–2010, we observed high densities of reindeer along the coast of eastern Finnmark, an area without traditional winter pastures. The precise areas used as winter grazing areas were confirmed by local authorities (Eira, H. Personal communication) and associated kill rate periods were accordingly assigned as high winter reindeer density in this special situation. Kill rate periods that span periods with changes in season or demographic status were split. If a period was still >2 months (only store-onboard collars) it was further divided into two equal periods to be comparable with preset kill rate periods ( $\leq 42$  days) used with the other collar types. In the analyses, we only included kill rate periods that we judged to be of high quality; i.e. with  $\geq 17$  continuous days of monitoring and cluster visits,  $\geq 7$  GPS-locations a day (Table S1) and where the GPS-collars functioned as expected. Initial analyses have shown that seven locations a day is needed to find the majority of the kills and 17 days was set as a cut-off to balance our desire to have good quality and sufficient quantities of data. Because these studies have been spread over many years with different sampling protocols, developing technology and increasing experience it was not possible to set a more consistent and objective cut-off.

### 3.3. Statistical analyses

To model the variation in the number of reindeer killed by individual lynx during a given time interval (rescaled to 30 days for presentations), we compared a set of zero-inflated negative binomial models (ZINB; Zuur et al., 2009) and evaluated their performance based on AIC values (Burnham and Anderson, 2002). A ZINB model is a mixture model consisting of two parts; a binomial model, with or without covariates, used to model the excess zeros, and a count process, including expected zeros, modelled by a negative binomial GLM (Zuur et al., 2009). The choice of the ZINB model

was justified by (1) the existence of excess zeros compared to a Poisson distribution, which made a zero-inflated model necessary and (2) excessive variation in the count process, which made a negative binomial model more appropriate than a Poisson model (ZIP; Likelihood ratio test,  $\chi^2 = 18.93$ ,  $df = 1$ ,  $p < 0.0001$ ). The number of monitoring days in a kill rate period did not affect the probability of zeros (glm,  $z = -1.15$ ,  $p = 0.25$ ). Although we had repeated observations for some lynx individuals (1–9 observations/lynx), we could not treat individual as a random factor to avoid pseudoreplication (Hurlbert, 1984), primarily because there is currently no generally accepted statistical method within software packages to deal with autocorrelated error structures in ZINB models within a frequentist framework (Zuur et al., 2009) and secondly, other sources of spatial and temporal auto-correlation would make the inclusion of individuals as random terms arbitrary.

We used a set of 25 biologically sound models to examine variation in kill rates. In the global model we included lynx social status and indicators of ecological conditions (season and reindeer density) with both terms plus their interaction included in both the binomial part and the count process of the model. We compared the global model with less complex models based on their AIC values. Finally, we compared the selected model from the subset described above with a model where sex of the lynx (males and females) was used instead of social status. In all models, log (number of monitoring days) was used as an offset variable, and all models were run in R 2.8.1 (R Development Core Team, 2010) with the add-on library *pscl* (Zeileis et al., 2008) using the command *zeroinfl*. Likelihood ratio tests for comparing models were performed with the command *lrtest* in the add-on library *lmtree* (Zeileis and Hothorn, 2002).

## 4. Results

We found 1443 prey remains at lynx clusters, the majority being reindeer (70%, Table 1). All monitored lynx had access to free ranging reindeer in their annual home ranges and all individuals killed reindeer. In comparison, only eight of the 18 lynx that had sheep available were documented as having killed sheep. Multiple reindeer kills were rare (5.5% of killing events), with 85% of them including two reindeer and 15% three reindeer. Multiple killing was not dominated by any sex or social status of lynx (Likelihood ratio test,  $G = 1.72$ ,  $df = 2$ ,  $p = 0.42$ ). At high reindeer density, the proportion of reindeer among the kills found was higher in winter than in summer (Likelihood ratio test,  $G = 61.37$ ,  $df = 1$ ,  $p < 0.0001$ ; Table 1). Even in winters when reindeer density was low (i.e. when herders had moved their flock to other grazing areas and none or only stray animals remained), 15% of the kills were reindeer. In contrast, 29% of the lynx (10 out of 35; all females) had at least one kill rate period where they did not kill any reindeer although reindeer density was high. In summer, 67% of all killed reindeer were calves and in winter 42% of known age kills were calves.

Among the 25 ZINB-models used to model variation in lynx kill rates on reindeer (Table 2), the model with the lowest AIC value ( $\Phi 11$ ) included the effect of social status in the binomial part of the model, and the main effect of social status and ecological conditions (season and reindeer density) as well as their interaction in the count part. The differences in AIC values between  $\Phi 11$  and the next ranked models ( $\Phi 6$  and  $\Phi 21$ ) were 2.4 and 2.6 respectively. This suggests that all three models should be considered (Burnham and Anderson, 2002). A likelihood ratio test implied that  $\Phi 11$  is supported over the more complex model where ecological conditions is also included in the binomial part ( $\Phi 6$ ;  $\chi^2 = 1.64$ ,  $df = 2$ ,  $p = 0.44$ ) while the difference between  $\Phi 11$  and the less complex  $\Phi 21$  (only intercept in binomial part) was significant ( $\chi^2 = 6.56$ ,  $df = 2$ ,  $p = 0.038$ ). The fourth ( $\Phi 16$ ) and fifth ranked model ( $\Phi 1$ ) had sub-

**Table 2**

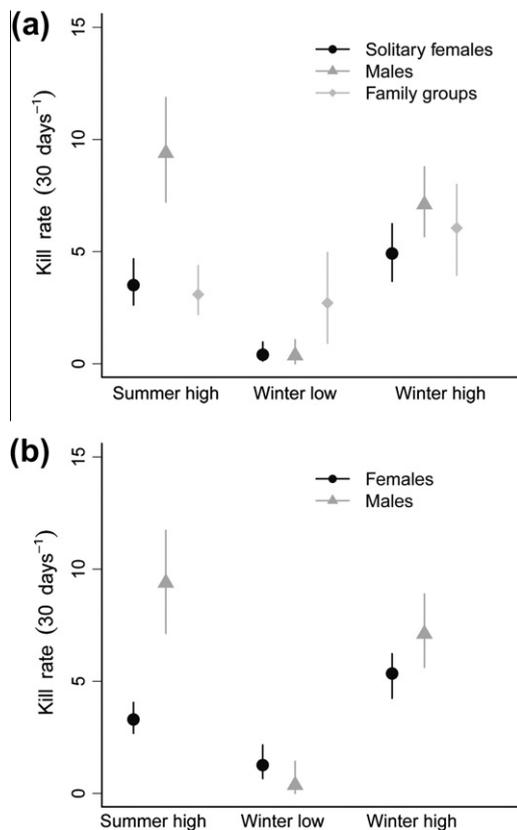
ZINB-models evaluated to assess the affect of lynx social status (Social): solitary females, family groups and males, and ecological condition (Ecol.): season and reindeer density (three levels: summer high, winter low and winter high), on kill rates. The models were evaluated based on the Akaike Information Criterion, and Akaike weights ( $w_i$ ) were calculated as described in Burnham and Anderson (2002).

Model	Count process model	Binomial model	df	AIC	$\Delta$ AIC	$w_i$
$\Phi$ 11	Social + Ecol. + Social:Ecol.	Social	13	612.6	0	0.562
$\Phi$ 6	Social + Ecol. + Social:Ecol.	Social + Ecol.	15	614.9	2.4	0.172
$\Phi$ 21	Social + Ecol. + Social:Ecol.	Intercept only	11	615.1	2.6	0.156
$\Phi$ 16	Social + Ecol. + Social:Ecol.	Ecol.	13	617.3	4.8	0.051
$\Phi$ 1	Social + Ecol. + Social:Ecol.	Social + Ecol. + Social:Ecol.	19	617.4	4.9	0.049
$\Phi$ 2	Social + Ecol.	Social + Ecol. + Social:Ecol.	15	622	9.5	0.005
$\Phi$ 17	Social + Ecol.	Ecol.	9	624.4	11.8	0.002
$\Phi$ 7	Social + Ecol.	Social + Ecol.	11	625.4	12.9	0.001
$\Phi$ 12	Social + Ecol.	Social	9	625.7	13.2	0.001
$\Phi$ 3	Social	Social + Ecol. + Social:Ecol.	13	626.9	14.4	0.000
$\Phi$ 22	Social + Ecol.	Intercept only	7	628.1	15.6	0.000
$\Phi$ 18	Social	Ecol.	7	628.9	16.3	0.000
$\Phi$ 8	Social	Social + Ecol.	9	630.2	17.7	0.000
$\Phi$ 4	Ecol.	Social + Ecol. + Social:Ecol.	13	633.7	21.2	0.000
$\Phi$ 14	Ecol.	Social	7	636.2	23.7	0.000
$\Phi$ 9	Ecol.	Social + Ecol.	9	636.6	24	0.000
$\Phi$ 19	Ecol.	Ecol.	7	636.9	24.4	0.000
$\Phi$ 5	Intercept only	Social + Ecol. + Social:Ecol.	11	639.1	26.5	0.000
$\Phi$ 24	Ecol.	Intercept only	5	639.8	27.2	0.000
$\Phi$ 20	Intercept only	Ecol.	5	641.9	29.4	0.000
$\Phi$ 10	Intercept only	Social + Ecol.	7	642.6	30	0.000
$\Phi$ 13	Social	Social	7	645.1	32.5	0.000
$\Phi$ 23	Social	Intercept only	5	645.4	32.9	0.000
$\Phi$ 15	Intercept only	Social	5	656.1	43.6	0.000
$\Phi$ 25	Intercept only	Intercept only	3	657.7	45.2	0.000

stantially less support ( $\Delta$ AIC = 4.8 and 4.9, respectively). Replacing social status from the best model ( $\Phi$ 11) with lynx sex gave only

marginally less support ( $\Delta$ AIC = 0.94) suggesting that sex is almost as good a predictor for lynx kill rates as social status. Separating among females by their reproductive status only affected kill rates in winter in areas with low reindeer density (Fig. 2a and b).

We observed a high variation in lynx kill rate on reindeer. The best performing model suggested that kill rates were dependent



**Fig. 2.** Predicted lynx kill rate on reindeer with 95% bootstrap confidence interval based on 128 kill rate periods from 35 lynx in northern Scandinavia in 2005–2010, separated by lynx social status (a) and sex (b). High-low indicates presence-absence of reindeer grazing areas within the lynx home range at the time of the kill rate period.

**Table 3**

Parameter values for the selected model in the subset described above (status:  $\Phi$ 11, Table 2) and the same subset where status was replaced by sex (sex). Parameter estimates are based on a contrast matrix, with the intercept in the count process model represented by solitary females (or females) during summer high, the main effect represent the effects of covariates compared with the intercept.

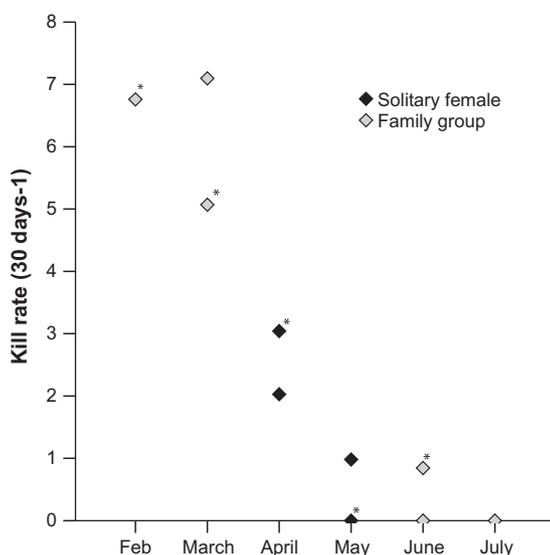
Model term	Parameter value ( $\beta$ )	SE	z-Value	p-Value
<b>Status</b>				
Count process model				
Intercept	-2.019	0.148	-13.62	<0.001
Winter low	-2.154	0.634	-3.40	<0.001
Winter high	0.337	0.196	1.72	0.085
Family groups	-0.108	0.251	-0.43	0.668
Males	0.858	0.196	4.38	<0.001
Winter low: family groups	2.022	0.778	2.60	0.009
Winter high: family groups	0.335	0.314	1.07	0.286
Winter low: males	-1.094	1.211	-0.90	0.367
Winter high: males	-0.617	0.264	-2.34	0.019
Zero-inflation model				
Intercept	-2.011	0.532	-3.78	<0.001
Family groups	0.152	0.828	0.18	0.854
Males	-13.556	411.698	-0.03	0.974
<b>Sex</b>				
Count process model				
Intercept	-2.057	0.121	-16.95	<0.001
Winter low	-0.956	0.382	-2.50	0.012
Winter high	0.484	0.153	3.16	0.002
Males	0.895	0.178	5.03	<0.001
Winter low:males	-2.289	1.103	-2.08	0.038
Winter high:males	-0.761	0.342	-3.22	0.001
Zero-inflation model				
Intercept	-1.819	0.407	-4.47	<0.001
Males	-9.093	40.149	-0.23	0.821

on ecological conditions (season and reindeer density), but also that lynx of different social status responded differently to the ecological conditions (Fig. 2a; Table 3). Overall, kill rates were highest in winter when reindeer density was high, but the highest individual kill rates were observed for male lynx in summer with high reindeer density. Here, the highest individual kill rates (above average) contained 55–95% calves. Kill rates were lowest during winter with low reindeer density within lynx home ranges but this was more pronounced for males and solitary females than for family groups. Family groups killed almost as many reindeer during winters with low reindeer density as during summers with high reindeer density although the variation was high.

## 5. Discussion

Semi-domestic reindeer are clearly the most important prey for lynx across all the areas where we conducted this study. All monitored lynx killed reindeer and we had no indications of the existence of a problem sex as observed for lynx depredation on sheep (Odden et al., 2002). Males had higher kill rates than females, similar to other studies on carnivore depredation on livestock (see Linnell et al., 1999 for a review) but this was only observed in summer. Multiple killing events were rare and were not dominated by any sex, although the degree to which individual kills were consumed was variable and often low, indicating a certain functional degree of surplus killing (Odden et al., 2010). Even though some lynx may kill many reindeer during parts of the year, others can apparently switch completely to small prey even at high density of reindeer. For example, we observed reduced kill rates on reindeer by female lynx both after separation of family groups in spring and during the weeks after giving birth (late May–mid-June; Fig. 3); when females are restricted in their movement (sensu Laurenson, 1995), spend most time at the natal lair (Schmidt, 1998), and decrease the time for hunting.

Despite this heavy use of reindeer, lynx are able to survive periods without reindeer by switching to other prey. In western Finnmark, lynx survived winters by preying on hares, birds and



**Fig. 3.** Effects of season and social status on lynx kill rate on semi-domestic reindeer illustrated by two female lynx (\* indicate same individual) in Tornedalen, Sweden, 2007. Reindeer density was high year around, but are widely distributed during summer (May–July) and aggregated around supplemental feeding grounds close to settlements during winter (February–April). The lynx did not kill reindeer at feeding grounds. High density of small non-ungulate prey was observed in the area and of 61 kills we found 33 small prey killed by the lynx between April–July.

mesopredators, like red fox and domestic cats (*Felis catus*), which were not so common in lynx diet in study areas where other ungulates are available (Odden et al., 2006). The few scavenging events observed (Table 1) were mostly confined to this area suggesting that few reindeer remained. Although lynx can survive on small prey the inclusion of ungulates in their diet likely improves fitness (Pulliainen et al., 1995). We found surprisingly high kill rates for family groups even when reindeer were supposed to be largely absent (Fig. 2a). Unfortunately it was logistically impossible to obtain any estimate, or even an index, of the numbers of stray reindeer that remained in these areas.

Lynx are known to be efficient predators and kill rates on ungulates remain high even at very low prey densities (Nilsen et al., 2009), a finding also confirmed by our study. Although we were able to explain parts of the observed variation in kill rate by including social status, season and reindeer occurrence in the models, much variation remains unexplained. Individual differences (Linnell et al., 1999; Nilsen et al., 2009), density and condition of reindeer (Tveraa et al., 2003), alternative prey densities (Odden et al., unpublished), area (Björvall et al., 1990), scavengers (Mattisson et al., in press) or human disturbance (Zimmermann et al., 2007) could all play a significant role but we were not able to test for them. In some areas, we observed much disturbance at kills from reindeer herders which likely decreased consumption and thereby increased kill rate. However, in Norway compensation is dependent on documenting causes of death forcing herders to find fresh kills in order to have the cause of death verified. Lynx predation on reindeer differs from predation on both domestic sheep and roe deer (Odden et al., 2006; Nilsen et al., 2009) in several aspects, which imply that extrapolation from other studies or species may be difficult. Lynx depredation on sheep is dominated by males, multiple and surplus killing is common, and sheep are mainly killed by lynx incidentally when encountered during other activities (Odden et al., 2002, 2008). In contrast, lynx actively search for reindeer and roe deer (Odden et al., 2006). Kill rates on reindeer seem to fluctuate more than for roe deer, although the mean kill rate is similar (Okarma et al., 1997; Nilsen et al., 2009). Reindeer occur more clumped than roe deer and their presence is less predictable and can vary from none to extremely high densities in a short period of time.

GPS-collars have greatly improved the quality of kill rate estimates (Knopff et al., 2009) but there are still some methodological uncertainties. In this study, we may have both over- or underestimated kill rates. It was not possible to evaluate if the probability of including reindeer that are not killed by the lynx but are found dead at a single lynx GPS-location, is higher or lower than the probability to miss reindeer killed by lynx but not fed upon (i.e. not forming clusters). Overestimation is supported by snow tracking of lynx that showed that lynx often visited reindeer carcasses that were neither killed nor fed upon by them (Haglund, 1966). In addition, 4% of lynx-killed reindeer in Sarek were visited by a second lynx (Odden et al., 2010), of which 58% formed clusters. On the other hand, the risk of underestimating kill rates is increased if we failed to locate prey remains even though clusters were formed. This risk increases for young calves, if clusters are covered with snow, or if scavengers have removed the majority of the prey remains. Altogether, we are still confident that our estimates are within acceptable errors, further supported by snow-tracking data (Pedersen et al., 1999).

Despite the high variation in lynx kill rate on reindeer reported here there is no doubt that lynx depredation has a large impact on reindeer management. Reindeer herders have expressed a certain willingness to accept low levels of depredation by carnivores (National Association of Swedish Sami, SSR), if economically compensated. However, this tolerance level is believed by many herders to be far exceeded today. Many herders argue that

compensation payments do not cover their losses. Reindeer husbandry covers large parts of the Scandinavian countries and to maintain the overall lynx population at the level set by national management goals, lynx cannot be excluded from this area. Semi-domestic reindeer are free-ranging and migrate over large areas and few efficient damage prevention measures exist that could be applied to the modern day extensive herding system (Mattisson et al., 2007). Keeping reindeer females in enclosures during calving and for the subsequent weeks is one of the few measures that have been shown to reduce overall levels of calf depredation by large predators (Kjelvik et al., 2000; Tveraa et al., 2003). The highest kill rates that we observed were in late spring when reindeer just returned to areas that had been empty of reindeer during winter, suddenly providing a super-abundance of reindeer with small calves. The observed increase in kill rates during summer for male lynx, which included a high proportion of small calves, suggests that enclosures may partly reduce depredation during this period when the risk of surplus killing is greatest because of the vulnerability of these neonatal reindeer. As long as political goals for lynx conservation require that lynx occur in the reindeer husbandry areas it is important from an energetic point of view that they continue to have access to reindeer as prey. As a consequence it is not desirable, even if it was possible, to completely stop depredation, but rather limit depredation to levels that are considered acceptable and ensure that fair compensation is paid which requires good data on individual kill rates.

Our results may not be applicable to the entire reindeer husbandry area in Scandinavia, as we monitored relatively few individual lynx in forested areas and none in areas where significant densities of roe deer occurred as a potential alternative prey. In small parts of the husbandry area reindeer coexist with roe deer, and here lynx seem to prefer roe deer even when reindeer densities are 10 times greater (Sunde et al., 2000; Moa et al., 2006). The density and body condition of reindeer varies dramatically across northern Scandinavia which may also influence lynx kill rates, although lynx are such an effective predator on reindeer (Haglund, 1966; Pedersen et al., 1999) that we also need to be open for the possibility that hunting success is not very dependent on reindeer condition.

## 6. Implications for compensations schemes

Often, and Scandinavia is not an exception, conflicts surrounding livestock depredation are largely influenced by disagreement regarding actual depredation levels. The results from this study constitute one of the first steps required to obtain the relevant knowledge of lynx impact on semi-domestic reindeer. We present the first quantification of the range within which lynx predation is likely to occur based on studying the predation patterns of individual lynx, rather than from examining the proportion of reindeer losses (Kjelvik et al., 2000). Our results also provide knowledge about factors causing spatial and temporal variation in lynx kill rates on reindeer. Altogether, this information can be used to evaluate current compensation levels based on empirical data, instead of a qualified guess of estimated losses as it is today. Our present data are sufficient to scale compensation payments to lynx density over large areas and over longer periods of time. This will hopefully lead to a reduction in conflict level concerning the overall potential impacts that lynx have on reindeer; relevant for both risk-based and ex-post compensation systems practiced in Sweden and Norway, respectively. For example, in Norway in 2008/2009, reindeer owners claimed compensation for three times as many reindeer ( $n = 64,855$ ) as the Norwegian government actually paid for ( $n = 20,742$ ; Norwegian Directorate for Nature Management: <http://www.rovvaltportalen.no/>) and of these, only 6% were de-

tected and confirmed as being killed by a predator. This illustrates a strong disagreement about the actual damage caused by the carnivores and the problem with low damage detection. This low detection rate, particularly during the snow free season, is caused by a widely distributed lynx predation on free ranging reindeer and highlights a major weakness of the ex post compensation scheme (Schwerdtner and Gruber, 2007). To compensate for a very low detection rate and to estimate actual level of losses, individual kill rate data in combination with lynx density estimates is essential. Using a risk-based compensation scheme excludes the need of damage detection but still requires good estimates of damage. Our findings reveal a high variation in kill rate estimates, which implies that there may be considerable fine scale (temporal and spatial) variation around this average at the level of the individual herder, which can make also a risk-based compensation system unfair. However, reindeer owners in Sweden have accepted and prefer the risk-based compensation system, although they argue that the compensation is far too low (Swenson and Andrén, 2005). The risk-based compensation system also requires good population estimates of the lynx which will facilitate management of lynx populations in reindeer husbandry areas, and could indirectly benefit conservation of the lynx in Scandinavia. The conservation of lynx can also directly benefit from a risk based systems as reindeer herders are compensated for including carnivores in their grazing areas, regardless of the levels of losses, which may decrease poaching (Andrén et al., 2006; Persson et al., 2009). Furthermore, in a risk-based compensation system, the reindeer owner can focus on reindeer husbandry, instead of searching for reindeer killed by lynx. There is also an incentive for the reindeer owners to invest in mitigation measures to reduce the losses, e.g. keeping reindeer females in enclosures during calving and the subsequent weeks. Because of the advantages of a risk based scheme in the reindeer husbandry area, Norway is currently considering moving into a risk-based compensation system and estimates of individual kill rate are essential in this process (Herfindal et al., 2011). There are other factors that, if included in future analyses, could potentially contribute to a more accurate prediction at finer scales, and therefore make the risk-based compensation system fairer. These include uncertainties in family group censuses (Linnell et al., 2007), and in lynx densities i.e. the number of solitary females and males associated with each family group (Andrén et al., 2002), to what degree predation is additive or compensatory (Tveraa et al., 2003) and weather conditions that may influence predation behaviour and reindeer vulnerability (Nilsen et al., 2009). However, the practicality of building such complex models requires both further lynx centric research across a wider range of conditions and complimentary studies of reindeer demographics (Tveraa et al., 2007).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.09.004.

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