



## Brown bear predation on semi-domesticated reindeer and depredation compensations

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### ABSTRACT

The recovery and conservation of large carnivores can negatively impact the economy of traditional pastoralist societies, including indigenous reindeer (*Rangifer tarandus*) herding communities. Quantifying the magnitude of predation on livestock is critical to evaluating governmental carnivore compensation schemes. We collaborated with two Sámi herding communities in northern Sweden (2010–2012) to examine brown bear (*Ursus arctos*) predation patterns on semi-domesticated reindeer and quantify the economic impact of bear predation. Predation patterns were estimated by following 21 GPS proximity-collared bears and ~2500 transmitter-collared female reindeer during calving season. We calculated economic impact by multiplying the monetary value of reindeer by the expected number lost to bears. On average, bears killed 10.2 [8.6, 11.5] calves per bear, accounting for 39–62% of all calf mortality, while few adult reindeer were killed. Bear kill rates increased with time spent in the calving area, and varied widely by individual and reproductive status, e.g., females with cubs-of-the-year did not kill calves. Kill intervals increased over the parturition season, and were larger for sub-adults than adults. The mean reindeer calf predation rate was 16–27%, which resulted in an annual loss between ~£50,000 and ~£62,000 per herding group. Current compensation schemes for herding communities in Sweden are calculated as a fixed rate based on herding community land-area. The herding groups in our study were reimbursed for ~2% of realized monetary loss. Compensation schemes based on herding community area, rather than realized predation patterns, may be less effective at mitigating the economic impact of living with large carnivores.

### 1. Introduction

Conservation efforts and shifting attitudes have facilitated the partial recovery of several large carnivore populations across Europe

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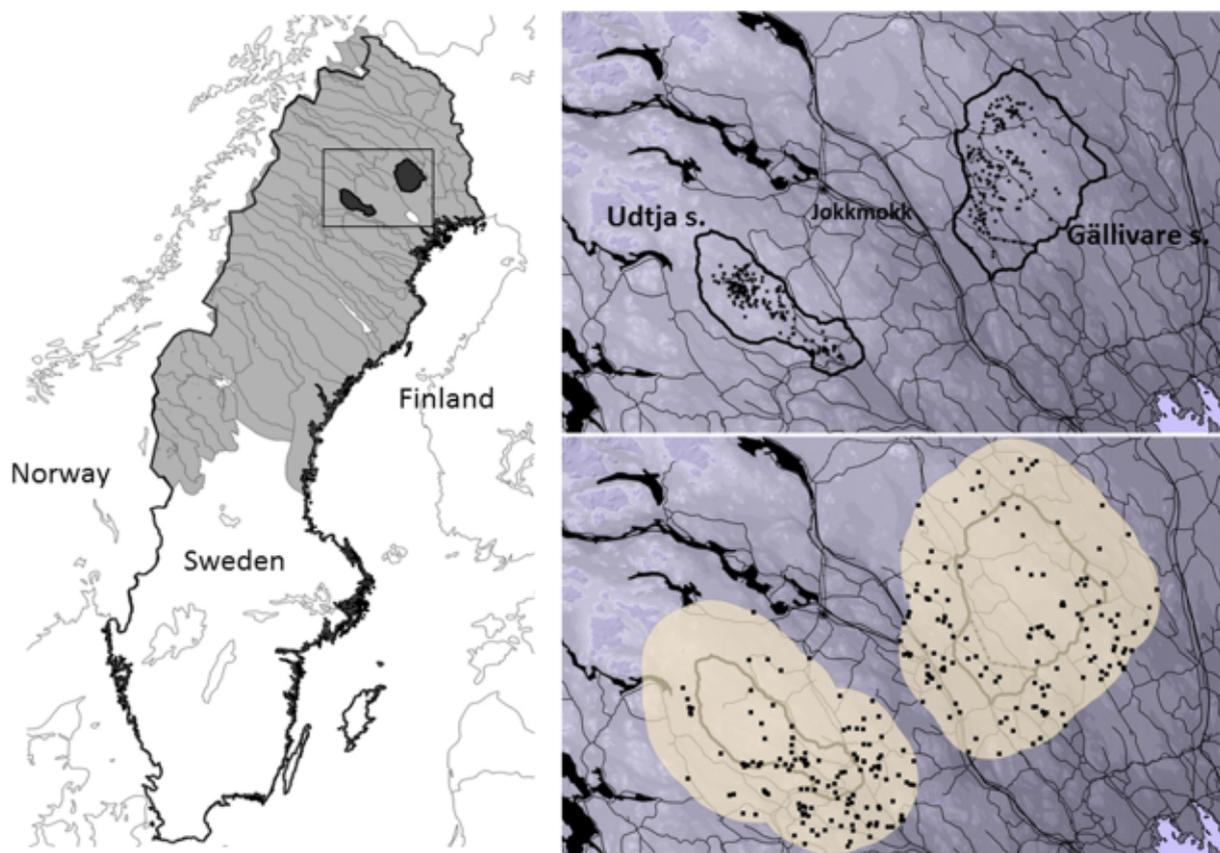
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over the last three decades (Chapron et al., 2014). However, the recovery of large carnivores can coincide with increased regional livestock depredations, which negatively impact local human livelihoods and fuel conflict (Graham et al., 2005; Heikkinen et al., 2011). This is especially problematic for traditional pastoralist societies whose culture and livelihood depend on livestock husbandry (e.g., Fox et al., 2004; Pape and Löffler, 2012; Van Eeden et al., 2018). For pastoralist societies already at risk from a host of threats (e.g., Dong et al., 2011; Easdale and Aguiar, 2018; Pape and Löffler, 2012), carnivore recovery may exacerbate the challenges of maintaining their traditional way of life.

Reindeer (*Rangifer tarandus tarandus*) herding is an important form of traditional nomadic pastoralism practiced by more than 30 different indigenous groups across the Arctic (Sköld, 2015). The Sámi, inhabiting northern Europe (i.e., Norway, Sweden, Finland and Russia's Kola Peninsula), are characteristic of the many indigenous peoples practicing reindeer herding (Sköld, 2015). However, the economic impact of predators on reindeer herding has steadily increased in parallel with the recovery of large carnivore populations in northern Europe, which influences the livelihood of herders (Hobbs et al., 2012; Pekkarinen et al., 2020; Rasmus et al., 2020; Sköld, 2015). Brown bears (*Ursus arctos*), which are an important predator of neonate ungulates (Nieminen, 2010; Rauset et al., 2012; Swenson et al., 2007), including reindeer and caribou (Adams et al., 1995; Jenkins and Barten, 2005; Nieminen et al., 2013), have recently recovered throughout much of the region (Chapron et al., 2014).

Multiple reindeer herding communities in Fennoscandia and Russia currently overlap with brown bear populations, where bears predominantly prey on reindeer calves during the parturition season (Nieminen et al., 2013). For herders, the loss of reindeer calves to carnivores means loss in both short- and long-term production, as calves provide annual profits during fall slaughter and supply the next generation of herd animals (Pekkarinen et al., 2020). Yet, the realized economic impact of brown bears on reindeer herding communities has been difficult to estimate. For example, most studies on bear-calf predation in Fennoscandia examined reindeer calf mortality from 1 to 2 months of age (e.g., Bjärvall et al., 1990; Norberg et al., 2006; Tveraa et al., 2003), excluding the most important age-class, neonates, from kill rate estimates. Moreover, bear predation on small and spatially scattered reindeer calves is an elusive process that is difficult to accurately assess, and there are currently no reliable estimates of bear-neonate reindeer kill rates available.

In Sweden, reindeer herders have repeatedly reported a substantial loss of calves due to bears, but the paucity of data on local bear predation patterns has made compensations politically challenging. In addition, Sweden has signed multiple international agreements designed to safeguard the future of both the Sámi culture and large carnivore populations (Nilsson-Dahlström, 2003). To facilitate this



**Fig. 1.** Map of the (a) study area with the calving grounds of Udtja and Gällivare forest reindeer herding districts in Norrbotten, Sweden, (b) reindeer calf kill sites within the calving grounds, and (c) bear scats collected within the buffer zones around the calving grounds during the 2010 county-wide bear population inventory.

dual conservation goal, Sweden implemented a revised conservation compensation program for large carnivores in 1996 (Persson et al., 2015; Zabel and Holm-Müller, 2008). The compensation scheme for brown bear depredation on semi-domesticated reindeer in Sweden is based on the land area size of the herding community, and there is currently an ongoing political process to revise this compensation scheme and align it with actual bear-induced reindeer losses. In order to make informed, evidence-based decisions for revising compensation schemes, the Swedish government commissioned this study to better understand bear predation patterns on semi-domesticated reindeer and quantify their economic impact.

We collaborated with two Sámi reindeer herding communities situated in Sweden's northern boreal forest between 2010 and 2012 to examine bear predation patterns and evaluate its economic impact on reindeer production. Close collaboration with Sámi herding communities facilitated the incorporation of traditional knowledge in study design and implementation. For example, we chose our study areas because traditional knowledge suggested that Sámi herding communities in the boreal forest experienced greater calf losses to bears than mountain communities. To evaluate bear predation patterns and estimate kill rates, we conducted predation studies using GPS-proximity-collared bears and transmitter-collared pregnant female reindeer. The aim was to assess temporal patterns of predation, evaluate variation in individual bear kill rates, estimate mean bear kill rates, and calculate the magnitude and economic impact of reindeer loss caused by bear predation. Based on our results, we propose a revised compensation scheme for herding communities in Sweden that overlap brown bear range.

## 2. Materials and methods

### 2.1. Study area

The reindeer herding area in Sweden covers 55% of the country, and is administratively organized in 51 herding communities (Fig. 1a). Communities are generally separated by natural barriers, such as rivers and topography, but fences are also sometimes used. There are 33 mountain herding communities where reindeer migrate between mountain summer pastures and winter forest pastures, and 18 herding communities where reindeer reside in the forest year-round, moving between higher elevation forest pastures in summer to lower elevation forests in winter. Reindeer calves are born in 'calving grounds' situated within the summer pastures between May and early June, with peak calving in mid-May (Holand et al., 2003).

This study was conducted in the summer range of two Sámi forest herding communities, Udtja and Gällivare, in Norrbotten County, Sweden (20° E 66° N; Fig. 1a).

Herding communities are divided into several 'Siidas'; Siida is the Sámi word for a reindeer herding group commonly, but not exclusively, formed by a family unit. The study was conducted in the Udtja and Purnu Siidas; hereafter referred to as Udtja and Gällivare, respectively. Udtja and Gällivare occupy the north-western part of the Eurasian taiga where the climate is continental, ranging from cold winters with deep snow to dry and temperate summers. The forest is mainly coniferous, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), interspersed by large bogs and wetlands with an understory of lichen (*Cladina* sp.) and ericaceous heather (*Ericaceae* sp.). The landscape is flat to gently rolling, and the elevation ranges between 13 and 714 m. The human population is relatively low ( $\bar{x}$  = 0.02 people per km<sup>2</sup>), with few human settlements and infrastructure ( $\bar{x}$  = 0.37 km roads per km<sup>2</sup>), although large parts of the forest are subject to intensive forestry.

Both Udtja and Gällivare herding communities have reported high losses of reindeer calves to bears, while lynx and wolverine predation were not considered a primary concern by the local reindeer herders, i.e., local lynx and wolverine abundances were low. The estimated brown bear population in Sweden increased from ~294 bears in 1942, to ~834 in 1993, peaked at ~3298 in 2008, declined to ~2782 bears by 2013, and remained relatively steady thereafter (Bischof et al., 2020; Swenson et al., 2017). In Sweden, reindeer herders are compensated for potential bear predation based on the land area of the herding community at a rate of approximately €7 per km<sup>2</sup>; the rate has remained the same since the 2009/2010 season (www.sametinget.se/rovdjur). Compensations are commonly then divided amongst the Siidas within each herding community.

### 2.2. Data collection

Bear predation studies were conducted between 2010 and 2012 in Udtja, and from 2011 to 2012 in Gällivare. We captured and collared bears via helicopter using established protocols (Arnemo et al., 2011), which were approved by the Swedish Ethical Committee on Animal Research; project ID C47/9 and C7/12. Bears were equipped with GPS proximity-collars (i.e., GPS-collars equipped with UHF receivers; Vectronic Aerospace GmbH, Berlin, Germany). Bear capture efforts were concentrated locally within each Siida in order to capture bears whose home range overlapped the calving grounds. Bear proximity collars were complemented by annually equipping pregnant female reindeer with trigger-transmitter collars (i.e., collars equipped with UHF transmitters; Vectronic Aerospace GmbH, Berlin, Germany). Pregnancy examinations were performed in late March or early April during the late winter round-up, and before spring migration, using rectal ultrasound (see Savelle et al., 2009). Bear collars were programmed to take GPS positions every 30 min, and increase to a fix rate of 1 position every 70 s for 1 h, when they came within 100 m of a trigger-collared reindeer (see Supplementary Information Section A). Based on local herder knowledge, we scheduled the proximity function on bear collars to remain active between 26 April to 24 September in 2010 and 2011. To save battery life, we narrowed that window to the actual observed predation period, with a buffer, of 26 April to 30 June in 2012.

In 2010, we visited all 70 s GPS positions; all of the 23 calf carcasses found in 2010 (Fig. 1b) were located in GPS clusters with  $\geq 3$  GPS positions within a 30 m radius. Thus, we used these parameters to define searchable clusters during the 2011/2012 study seasons. We aimed to visit each cluster the day after it was generated, or as soon as the bear left the site thereafter. Detected calf mortalities were

examined by field staff (at least 1 researcher and 1 herder), and cause of death was collaboratively determined following the local provincial ranger standards (see Skåtan and Lorentzen, 2011). We also noted reindeer age (calf/adult) and sex, and recorded time of death as the first location of the radio-collared bear within the cluster. If two or more bears created a temporally overlapping cluster at a kill site, the bear with the first GPS position at the carcass was judged to have killed the reindeer.

### 2.3. Data analysis

#### 2.3.1. Brown bear kill rate

We used zero-inflated negative binomial mixture models to estimate seasonal kill rate by bear demographic category using the 'pscl' package, version 1.4.9 (Jackman, 2010) in R (R Core Team, 2020). The model included two separate processes; one part to model excess zeros (here: the probability of killing zero calves), represented by a binomial distribution with a logit link, and a count part to model over-dispersed count outcomes (number of calves killed), represented by a negative binomial distribution with a log link (Zeileis et al., 2008). We estimated kill rate using the number of calves killed by individual bears as a response, and compared the effects of alternate combinations of demographic classes of bears: sex, age (adult/sub-adult) and reproductive status (female with cubs-of-the-year (FCOY), female with + 1 year old cubs (FY), lone female and lone male), as well as individual herding communities (Udtja/Gällivare).

FCOY did not kill any calves during the study, so we predicted zeroes in the demographic group FCOY to stem from a separate process compared to the other groups. For the other demographic groups, potential zeroes were predicted to stem from a random count process. Therefore, we included FCOY in the binomial part, but only the other demographic groups in the count part of the models. Because the collaring of female reindeer and registrations of kills were restricted to the calving grounds, whereas bears may roam outside those borders, we accounted for individual differences in time spent within the calving grounds; 'hours in calving grounds' was included as an offset variable, log transformed to match the link function. Model selection was done using second-order Akaike's Information Criteria (AICc), where the model with the lowest number of parameters with  $\Delta\text{AICc} < 2$  was considered the most parsimonious (Burnham and Anderson, 2002). For model predictions, we calculated kill rates relative to time spent within the calving grounds as a sequence from 0 to 991 h (i.e., maximum observed value) divided into intervals of 100, and provide bootstrapped 95% CIs. The mean kill rate was estimated from the top model using mean observed time across all demographic groups, except FCOY.

Kill intervals (i.e., time between consecutive kills) were calculated using only intervals between successively killed reindeer where the bear remained within the calving ground during the entire interval. The distribution of kill intervals was right-skewed, thus we estimated kill intervals using log-transformed time (minutes) between kills as a response variable in linear mixed effects models in R package 'lme4' (Bates and Maechler, 2014). We included Julian date as potential first and second order covariates, as well as bear demographic group. To account for potential individual effects and repeated observations from the same bear, we tested combinations of 'year', 'herding community', and 'bear individual' as random intercepts. We used the same principles for model selection and predictions as described for kill rate estimation.

#### 2.3.2. Economic impact

To assess the influence of bears on overall calf loss, we estimated the total number of reindeer calves killed by bears in each Siida, and compared this to the total reindeer calf mortality in the two Siida (calves died for reasons other than predation). Total calf mortality was estimated from observations of radio-collared reindeer during an annual calf-marking event in late June/early July, when females and calves were rounded up and counted. The rate of calf loss among the radio-collared females was then extrapolated to the total number of adult female reindeer in the Siida. To calculate of the total number of calves killed by bears within the two Siida, we multiplied estimated kill rates with the estimated number of bears located in each calving ground. Local bear numbers were estimated using scat collection (Fig. 1c) to detect individual DNA (see Supplementary Information Section A). We restricted this estimate to bear demographic categories that actively preyed on calves, i.e., we excluded FCOY and cubs  $\leq 2$  years old.

Finally, we estimated the net monetary loss due to bear predation by multiplying the total number of calves killed by bears with their mean monetary value, and subtracting that from the realized compensation payments for both Siida; we used a rate of 0.1 to convert SEK to Euro. For 2010, 2011, and 2012, reindeer calves were valued at €180, €177, and €165 ( $\bar{x}$  = €174), while adult female reindeer were valued at €369, €363, and €338 ( $\bar{x}$  = €357), respectively (www.sametinget.se/rovdjur). The comparable updated values for 2020 were €219 for calves and €450 for adult females. Udtja and Gällivare were paid €2261 and €5060 annually; the Siida that participated in our study in Udtja and Gällivare received €1130 and €1500 in 2013, respectively.

## 3. Results

Between 2010 and 2012, we fit 21 bears with GPS-UHF proximity-triggered collars and 2585 pregnant female reindeer with UHF transmitter collars. Collared reindeer represented 53%–100% of total females in the two herds (Table S7). Between 1 May and 15 June, we visited 1135 clusters on average 41 h after the bear left and found 374 reindeer carcasses (30 adult females; 344 calves) within the two calving grounds (Udtja = 206; Gällivare = 168). Of these, 350 carcasses were killed by radio-collared bears (17 adult females; 333 calves); the other carcasses were either too old to have been killed by the radio-collared bear ( $N = 17$ ), or died from other causes ( $N = 7$ ).

Most calves (90%) were killed in May, with predation peaking around 21 May (Fig. 2a). Almost 100% of calves (332/333) and 76% of adult females (13/17) were killed between 1 May and 15 June (Fig. 2a-b). During this period, the radio-collared bears stayed within the calving grounds for an average of  $21 \pm 14$  days ( $408 \pm 315$  h), and killed on average  $11 \pm 12$  calves and  $0.4 \pm 0.8$  adult females,

with an average interval of  $13 \pm 18$  h between consecutive calf kills (Table S1). Time spent on the calving grounds, the number of calves killed, and the mean length of time between consecutive kills varied between bear individuals, and across bear demographic categories (Table S1).

### 3.1. Brown bear kill rate

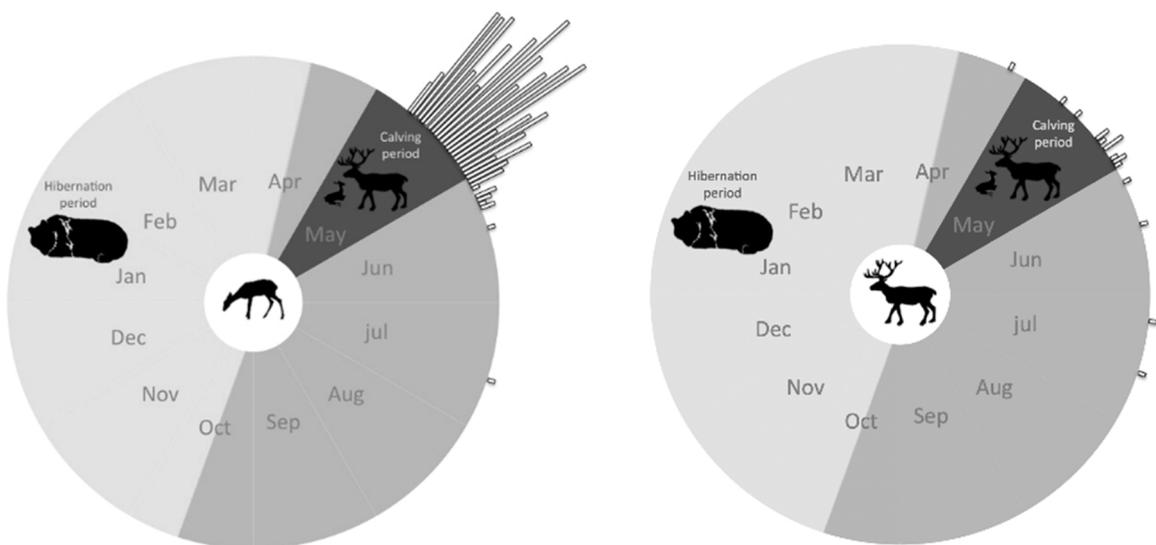
The top-ranked model estimating bear-calf kill rate included only FCOY in the binomial part, and only the intercept in the count part (Table S2). However, the offset variable ‘hours in calving grounds’ in the count model indicated that a large part of the observed variation in kill rates between demographic categories of bears could be attributed to differences in time spent in calving areas (Fig. 3; Table S3). The predicted mean kill rate of bears in calving grounds during the calving season was 10.2 [95% CI= 8.6, 11.5] calves, excluding FCOY that did not kill reindeer (Fig. 3). The total number of calves killed by an individual bear per season increased with the number of hours spent in the calving ground (Fig. 3). Accordingly, bears that remained in the calving area the maximum observed hours (991 h; Table S1) would have killed an estimated 26 [22.1, 29.1] calves (Fig. 3).

The top-ranked model estimating bear kill interval included Julian date as a first and second order variable and age class (adult/sub-adult) as fixed effects, and ‘bear individual’ as a random intercept (Table S4). Kill intervals increased over the season, and sub-adult bears had larger kill intervals than adults (Fig. 4; Table S5). Adult bears had a mean kill interval of 3.7 [2.0, 6.7] hours at the beginning of the season, which increased to 7.5 [2.7, 20.5] hours by the end of the season (Fig. 4).

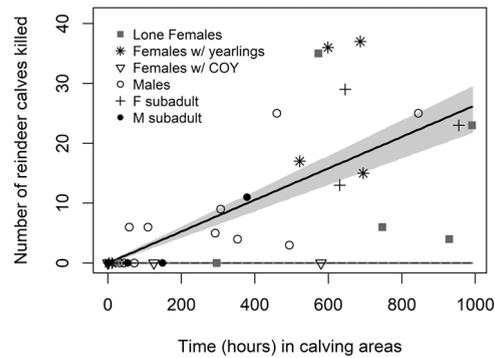
### 3.2. Economic impact

We estimated 71 [62–96] and 58 [53–75] bears used the calving grounds in the Udtja and Gällivare study areas, respectively; 32 and 26 were considered ‘active predators’ (Table 1, S6). The mean total calf mortality during the study period among radio-collared pregnant female reindeer was 43.0% ( $N = 2074$ ) in Udtja and 40.6% ( $N = 1420$ ) in Gällivare. With an average 1221 (1251, 1176, and 1235) and 1660 (1650 and 1669) adult female reindeer in Udtja and Gällivare Siidas per year during the study, this implies a total mortality of 524 and 674 calves, respectively. Our kill rate model predicted the number of calves killed by bears was 326 [275,368] in Udtja and 265 [224,299] in Gällivare (Table 1), which represented 62% [52%, 70%] and 39% [33%, 44%] of the estimated lost calves, with a subsequent overall predation rate of 27% [23%, 30%] and 16% [13%, 18%] in Udtja and Gällivare, respectively. Using 0.4, the mean adult female kill rate, we also estimated that bears killed 12.8 [11.1, 14.4] and 10.4 [8.8, 12.0] adult female reindeer per year in Udtja and Gällivare, respectively (Table 1).

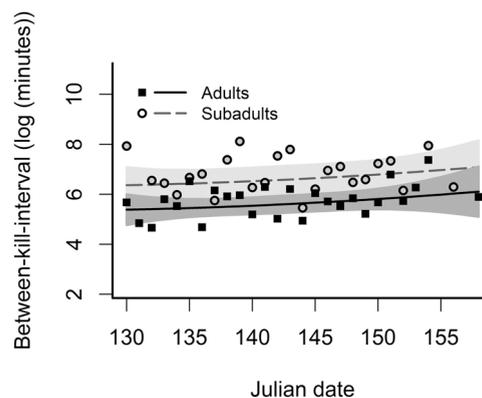
During our study, the loss of reindeer calves and adult females to bears cost the each participating Siida in Udtja and Gällivare approximately €61,192 and €49,740 per year (Table 1). Those Siida were annually compensated €1130 and €1500 by the Swedish government for bear predation, which covered about 2.4% of the total losses (Table 1). The net annual loss for Udtja and Gällivare, after compensation, was thus €60,062 and €48,240. The compensation scheme has remained stable since 2009, however, the value of calves has increased through time. Assuming conditions remained the same in 2020, the current net annual loss for Udtja and Gällivare would increase to €76,118 and €61,291, respectively, cutting the amount of loss compensated for to 1.9%.



**Fig. 2.** Number of (a) reindeer calves ( $N = 333$ ) and (b) adult female reindeer ( $N = 17$ ) killed per day by the 21 radio-collared bears throughout the year in the Udtja and Gällivare herding districts in Northern Sweden, 2010–2012. For reference, the year is split into the winter hibernation period (light gray), the summer period when bears are active (medium gray) and the reindeer parturition period (dark gray).



**Fig. 3.** The estimated mean number of reindeer calves killed during summer as a function of time (hours) bears spent within calving areas (i.e., the kill rate). Population-averaged fitted values and bootstrapped 95% CIs were generated using the highest ranked zero-inflated negative binomial model from the AICc model set (Table S2, S4); the dotted line represents females with cubs of the year and the solid line represents all other demographic categories of bears. Observed frequencies are provided as points representing different demographic classes of bears.



**Fig. 4.** Estimated between-kill-intervals in minutes (log-transformed) with 95% CI as a function of Julian date, based on the highest ranked mixed-effects model (Table S3, S5) in the calving grounds of Udtja and Gällivare forest reindeer herding districts in Northern Sweden, 2010–2012. Mean daily values of observed between-kill-intervals are given as points, divided among bear age groups.

#### 4. Discussion

Our results suggest that brown bears may prey heavily on neonate calves in reindeer calving grounds, and that current compensation schemes for reindeer herding communities in Sweden are suboptimal in terms of adequate reimbursement to mitigate the economic impact of living with bears. Bear predation accounted for 62% and 39% of all calf losses within the Udtja and Gällivare Siida, respectively. This resulted in a cumulative predation rate of 27% and 16%, and a net annual monetary loss of €61,192 and €49,740, respectively. Sweden's compensation program covered about 2.4% of the total calves lost to bear predation between 2010 and 2012, which dropped to < 2% in 2020.

We observed high reindeer calf predation rates by bears. Bears killed an average of 10.2 calves per bear per season (Fig. 3), accounting for up to 64% of all calf mortality between 2010 and 2012. Almost 98% of bear predation occurred between 1 May and 9 June, suggesting bears primarily targeted neonate reindeer calves within the first few weeks of life. These results are consistent with studies from other reindeer/caribou systems, which found brown bears primarily prey on neonates, and kill rates are highest during the parturition period (Adams et al., 1995; Jenkins and Barten, 2005; Nieminen et al., 2013). In Alaska, Brockman et al. (2017) estimated brown bears killed on average 14.1 caribou calves per season, which is slightly higher than our mean of 10.2. However, Brockman et al. (2017) may have overestimated kill rates, as they purposefully selected bears that were known to kill calves.

Predation on reindeer calves was limited in time, and was highly correlated with the pulse of newborn calves. After the parturition period ended in early June, calf predation functionally stopped. In Fennoscandia, bears generally switch to neonate moose (*Alces alces*) in mid-June, which are born slightly later than reindeer calves (Solberg et al., 2007; Twynham et al., 2021). Similar intense temporal predation pulses have also been observed in other systems where bears prey on neonate ungulates (e.g., Barber-Meyer et al., 2008; Rauset et al., 2012; Swenson et al., 2007), including neonate caribou (Adams et al., 1995; Jenkins and Barten, 2005). Kill intervals also increased over the calving season (i.e., kill rates decreased), likely due to the reduced vulnerability of calves coinciding with their progressively improving locomotive ability after birth (Jenkins and Barten, 2005; Lent, 1974). Our results also show that bears killed very few adult reindeer, < 2 per year, which is consistent with other research showing bears rarely prey on adult caribou (Zager and

**Table 1**

The estimated number of predatorily active bears in each Siida, number of calf and adult female reindeer killed by bears, the gross annual monetary loss from calf and adult female predation during the study (2010–2012) and now (2020), the annual compensation paid by the Swedish government, and the net annual monetary loss from calf and adult female predation during the study and now. The gross and net monetary losses are calculated by multiplying the mean number of calves and adult female reindeer killed annually by their mean monetary value. 95% CIs are shown in parentheses, monetary losses in red, and monetary gains in black.

	Udtja	Gällivare
Number of bears	32 (28, 42)	26 (24, 33)
Number of calves killed	326 (275,368)	265 (224,299)
Number of adult females killed	12.8 (11.2, 14.4)	10.4 (8.8, 12.0)
Gross annual monetary loss (2010-2012)	€61,192	€49,740
Gross annual monetary loss (2020)	€77,248	€62,791
Annual compensation	€1,130	€1,500
Net annual monetary loss (2010-2012)	€60,062	€48,240
Net annual monetary loss (2020)	€76,118	€61,291

Beecham, 2006). However, adult females were generally killed more often during the parturition period (Fig. 2b), possibly due to greater physical and behavioral vulnerability when calving.

We observed high variation in calf predation rates between bear individuals (Table S5). This corroborates that some bears are likely ‘specialists’, or more efficient at hunting reindeer calves than others (Linnell et al., 1999), which appears to be a common phenomenon across systems. For example, Brockman et al. (2017) found that some bears killed more than 30 calves during a season, while others killed few. Research from bear-moose predation studies in Scandinavia also suggests that calf selection varies widely between individuals (Ordiz et al., 2020). Interestingly, we detected no difference in kill rate between bear demographic categories, after controlling for time spent in the calving grounds, apart from females with cubs-of-the-year that did not prey on calves. This differs from some earlier studies on bears and other carnivores where demographic classes influenced prey selection and kill rates (e.g., Knopff et al., 2010; Mattisson et al., 2011; Young and McCabe, 1997), although Boertje et al. (1988) found no differences in caribou calf kill rate between demographic categories of bears. This could be because kill rates were driven more by individual variation than variation between demographic categories, and/or the low sample sizes of bear demographic categories in our study (Twynham et al., 2021). However, we also found that kill intervals were generally longer for sub-adult bears compared to adults (Fig. 4), likely because sub-adult carnivores are generally less experienced hunters (e.g., Holekamp et al., 1997; MacNulty et al., 2009).

Most GPS-based predation studies underestimate true kill rates, particularly with medium- and small-sized prey (Sand et al., 2005). Using proximity-triggered-collars is a seemingly more reliable method for evaluating predation patterns, however, our methodology was not without limitations. We therefore investigated the potential role of three major sources of uncertainty associated with our approach: (1) adult female reindeer lacking proximity collars, (2) unvisited clusters, and (3) radio-collared bears accompanied by unmarked bears, all of which could lead to a biased kill rate estimates (see Supplementary Information Section C for full evaluation and discussion). In short, we found the potential for over- and under-estimation was relatively small in our study; (1) a large proportion of pregnant female reindeer were radio-collared within each Siida (Table S7, Figs. S1-S2), (2) the potential error due to unvisited clusters was small (Table S8-S9, Fig. S4), and (3) assumed associations among marked and unmarked bears at kill sites was minor (Table S10-S11). Thus, we are confident our estimates of bear kill rates and kill intervals are sufficiently accurate. Interestingly, both our results, and those from Brockman et al. (2017), found higher bear-neonate ungulate kill rates than many earlier reported studies (Ballard et al., 1981; Boertje et al., 1988; Rauset et al., 2012; Swenson et al., 2007), likely due to new and more accurate survey methods.

In Udtja and Gällivare, bears killed approximately 326 and 265 reindeer calves per year, respectively (Table 1). These estimates are likely conservative, i.e., the upper 95% CI for local bear estimates was relatively high (Table S6), and there was large variation in kill rates between bear individuals, suggesting bear-induced neonate mortality could be higher than observed. The net monetary loss, after compensation, during our study was between €50,000 and €60,000 for each Siida per year (Table 1). Importantly, these estimates only account for direct losses from missed slaughter payments, and do not account for the indirect long-term loss of calf recruitment into the herd.

Currently, reindeer herding communities in Sweden are compensated for potential bear predation based on the communities land area (i.e., they are paid per km<sup>2</sup>; www.sametinget.se/rovdjur). Sweden’s compensation program paid €1130 and €1500 annually to the Siidas in our study to help alleviate the burden of bear predation, which covered the cost of approximately 6–8 calves, or about 2% of

their net monetary loss due to bears. The current compensation system is therefore under budget, and could possibly be skewed as well. Given the uneven distribution of bears on the landscape (Bischof et al., 2020), it is likely that herding communities that cover a large area and have relatively few bears benefit, while smaller villages with calving grounds in primary bear range and habitat lose out.

As part of our commissioned task by the Swedish government, we therefore propose a revised compensation system that should be more equitable for herding communities that coexist with different sized local brown bear populations. The new system should annually compensate each herding community in relation to the number of calves the local bear population is expected to kill (i.e., the kill rate multiplied by the local bear population), and the current valuation of calves at slaughter. In Sweden, the number of local bears are calculated based on DNA scat analysis collected during routine bear inventories that occur approximately every 5 years paid by the national government (Naturvårdsverket, 2016). Both the details of the revised compensation system, and the monitoring efforts necessary to provide data for the revised compensation scheme, could be further developed and implemented collaboratively with the reindeer herders.

## 5. Conclusions

Facilitating coexistence between large carnivores and traditional pastoralist societies is imperative for the conservation of wildlife populations and the preservation of traditional ways of living. We suggest that effective compensation schemes should be based on local carnivore population size and their expected offtake, rather than land-use area, as in the case of bears and semi-domesticated reindeer in Sweden, or *post-hoc* predation compensation as commonly used in other systems. Basing compensation schemes on land-use area, without taking into account the size of the carnivore population, may result in biased compensation such that those living with the most large carnivores endure the greatest financial hardship. Compensating for predation *post-hoc* can also be problematic, as the burden of proof often lies with the livestock holder, and predation can be difficult, time-consuming, and costly to prove (Engeman, 2000; Schwerdtner and Gruber, 2007). Yet, evaluating predator kill rates and local abundances takes time and money. Thus, monitoring efforts should be supported by respective national governments, and implemented in collaboration with the local people.

## Author Contributions

JF and OS coordinated the long-term study. JF, OS and PS conceived the study. JF, LTP, OS, PS, and RS planned, organized, and implemented field work. AS, GR, JF, JK, LTP, OS, PS, RS and TS participated in fieldwork and data collection; AT, GR, OS, TS carried out data management and statistical analysis; AT, OS, and TS wrote the manuscript. All authors helped draft the manuscript and gave final approval for publication.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Research data are available upon request. To request the data, contact the corresponding author of the article.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02168](https://doi.org/10.1016/j.gecco.2022.e02168).

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