


ARTICLE

Large carnivore conservation and traditional pastoralism: A case study on bear–reindeer predation mitigation measures

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Abstract

While wildlife and cultural preservation goals can be either complimentary or counteractive, the goals of large carnivore conservation and traditional pastoralist lifestyles are often at odds. Livestock depredation can negatively impact the economies of livestock herders, while subsequent lethal removals contribute to local carnivore population declines. Here, we collaborated with two Sámi reindeer herding communities (2010–2016) situated in Sweden's boreal forest to evaluate the efficacy and economic feasibility of three brown bear predation mitigation measures: corralling pregnant reindeer during parturition, lethal bear management removals, and public bear-license hunting. Calving corrals increased survival for reindeer calves born to average-sized females by 7%–15%, and by 14%–30% for calves born to small females. However, the realized cost of implementing calving corrals outweighed the financial gain for both our study areas (net losses ranged between €1111 and €6210 per calf saved from bear predation per year when using the updated 2021 calf value; 1€ [Euro] = US\$1.1), as well as for almost every theoretical scenario we explored (net losses €234 and €13,995 per calf saved from bear predation). The exception was the theoretical scenario where small herding communities overlapped large bear populations, which crossed the breakeven efficacy bear/reindeer ratio of 13.5 bears/100 reindeer and had a potential net gain of €36 per saved calf. Similarly, the cost of lethal management removals of bears outweighed the potential financial gain from saved calves, with net losses between €75 and €239 per calf. License hunting, where the hunters voluntarily incur the monetary costs of removing bears, is in most cases the only economically viable mitigation measure where the cost of mitigation did not outweigh the financial gain from increased reindeer survival. While the annual public license hunt was the most cost-effective mitigation measure, it may be less biologically effective, that is, bear hunting occurs in the fall and reindeer

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parturition the following spring which leaves time for the empty niche of harvested bears to be filled by survivors. Economically and biologically effective predation mitigation measures are key for promoting coexistence, and we suggest that potential mitigation measures should be studied in collaboration with local people.

KEYWORDS

brown bear, calving corrals, economic feasibility, management removal, predation, reindeer herding

INTRODUCTION

Global biodiversity and ecosystem health are declining rapidly, and the large-scale conservation of both wildlife species and ecosystem function has never been more critical (IPBES, 2019). This includes the recovery and conservation of large carnivores, who play a key ecological role in nature via their top-down effects on ecosystems (Terborgh et al., 2001; Wolf & Ripple, 2018). Although some populations have recovered in some areas (Bruskotter & Shelby, 2010; Chapron et al., 2014), most large carnivores remain severely threatened, largely due to habitat loss, prey depletion, and human persecution (Ripple et al., 2014). Traditional ways of life, including traditional indigenous pastoralist systems, are also under increasing risk worldwide from a range of threats including colonialization, urbanization, land-use change and conflicts, shifting market economics, pasture degradation, and climate change (e.g., Banjade & Paudel, 2008; Cambou et al., 2021; Dong et al., 2011; Easdale & Aguiar, 2018; Kassahun et al., 2008; Pape & Löffler, 2012; Skarin et al., 2018).

Wildlife and cultural preservation goals can be either complimentary or counteractive depending on the circumstance. For instance, Maasai pastoralist communities facilitate wildlife conservation in Tanzania via their local land and water management systems (Nelson, 2012). However, large carnivore conservation and traditional pastoralist lifestyles can also be at odds (e.g., Åhman et al., 2022; Fox et al., 2004; Pape & Löffler, 2012; Van Eeden et al., 2018). Livestock depredation can have a negative economic impact on traditional livestock husbandry (Støen et al., 2022). Subsequent retaliatory killings and lethal management actions result in local carnivore population declines, leaving some populations on the edge of viability (Inskip & Zimmermann, 2009; Kaczensky, 1999). Evidence-based understanding of the biological, cultural, and economic efficacy of predator mitigation measures is urgently needed to inform local policies and promote coexistence (Pooley et al., 2017; Van Eeden et al., 2018).

There are a variety of lethal and nonlethal mitigation measures used by both traditional and modern herding

communities to counteract livestock depredation. Lethal measures range from the targeted control of individual problem animals to large-scale predator removal programs that reduce, or functionally eradicate, local carnivore populations (Reynolds & Tapper, 1996; Woodroffe & Ginsberg, 1998). Nonlethal mitigation measures include livestock enclosures (e.g., Manoa & Mwaura, 2016; Ogada et al., 2003; Weise et al., 2018), guardian animals (e.g., dogs; Ivaşcu & Biro, 2020; Smith et al., 2000a), translocation of problem animals (Linnell et al., 1997), and a host of other deterrent techniques such as hazing and fladry (Smith et al., 2000b). Although not a predation mitigation measure per se, wildlife damage compensation programs are another useful tool that has the potential to facilitate coexistence (Morehouse et al., 2018; Ravenelle & Nyhus, 2017). However, the success of these mitigation measures is context dependent and can vary based on environmental conditions, carnivore life histories, and local cultural values (Pooley et al., 2017; Van Eeden et al., 2018). Thus, predation mitigation measures and coexistence strategies need to be both validated and cost-effective, as well as put into local cultural and environmental contexts (Eklund et al., 2017; Van Eeden et al., 2018).

Reindeer (*Rangifer tarandus tarandus*) herding is an important traditional form of nomadic pastoralism that is conducted by over 30 different indigenous groups across the Arctic nations (Sköld, 2015). Here, we define reindeer herding as the “control of free-ranging animals in terrain,” while husbandry is the “accumulation of profit” (Brännlund & Axelsson, 2011). Similar to other pastoralist lifestyles, the culture of reindeer herding and husbandry is at risk from an array of threats including land-use conflicts, shifting economic patterns, mining, large-scale human disasters (e.g., Chernobyl), climate change, as well as predator recolonization and recovery (Bostedt, 2001; Danell, 2000; Furberg et al., 2011; Herrmann et al., 2014; Parkatti & Tahvonen, 2020; Pekkarinen et al., 2020; Rasmus et al., 2020; Skarin et al., 2018). Large carnivores, including lynx (*Lynx lynx*), wolverine (*Gulo gulo*), wolves (*Canis lupus*), and brown bears (*Ursus arctos*), have

recently recovered and recolonized in parts of Europe (Chapron et al., 2014). Concurrently, the economic impact of predators on reindeer husbandry has increased over the last decades (Åhman et al., 2022; Pekkarinen et al., 2020; Rasmus et al., 2020; Sköld, 2015).

Brown bears are an important predator of neonate ungulate calves, including reindeer and caribou (Adams et al., 1995; Jenkins & Barten, 2005). Furthermore, the loss of neonates to brown bears is thought to be additive to other sources of predator-induced neonate mortality (Griffin et al., 2011), although this relationship remains unquantified for reindeer. Many herding communities in Fennoscandia and Russia overlap the brown bear range (Figure 1), where brown bears prey on reindeer calves predominantly during the calving season (Nieminen et al., 2013; Støen et al., 2022; Twynham et al., 2021). Calves of the year are critical to economically viable

reindeer husbandry, as they supply both the next generation of herd animals and deliver annual profits during slaughter (Pekkarinen et al., 2020). Traditional knowledge suggests that herding communities situated in boreal forests endure greater calf losses to brown bears than those in mountains in Scandinavia because (a) bears in Scandinavia are a forest-dwelling species, and (b) the dense forest and lack of continuous snow cover make it more difficult to monitor reindeer via snowmobile during the calving season compared to the high, open terrain in mountain herding communities (Støen et al., 2022).

The Sámi, who inhabit a broad area throughout parts of northern Norway, Sweden, Finland, and Russia's Kola Peninsula, are characteristic of the many indigenous peoples who practice reindeer herding and husbandry (Sköld, 2015). We collaborated with two Sámi herding communities situated in Sweden's boreal forest (Figure 1)

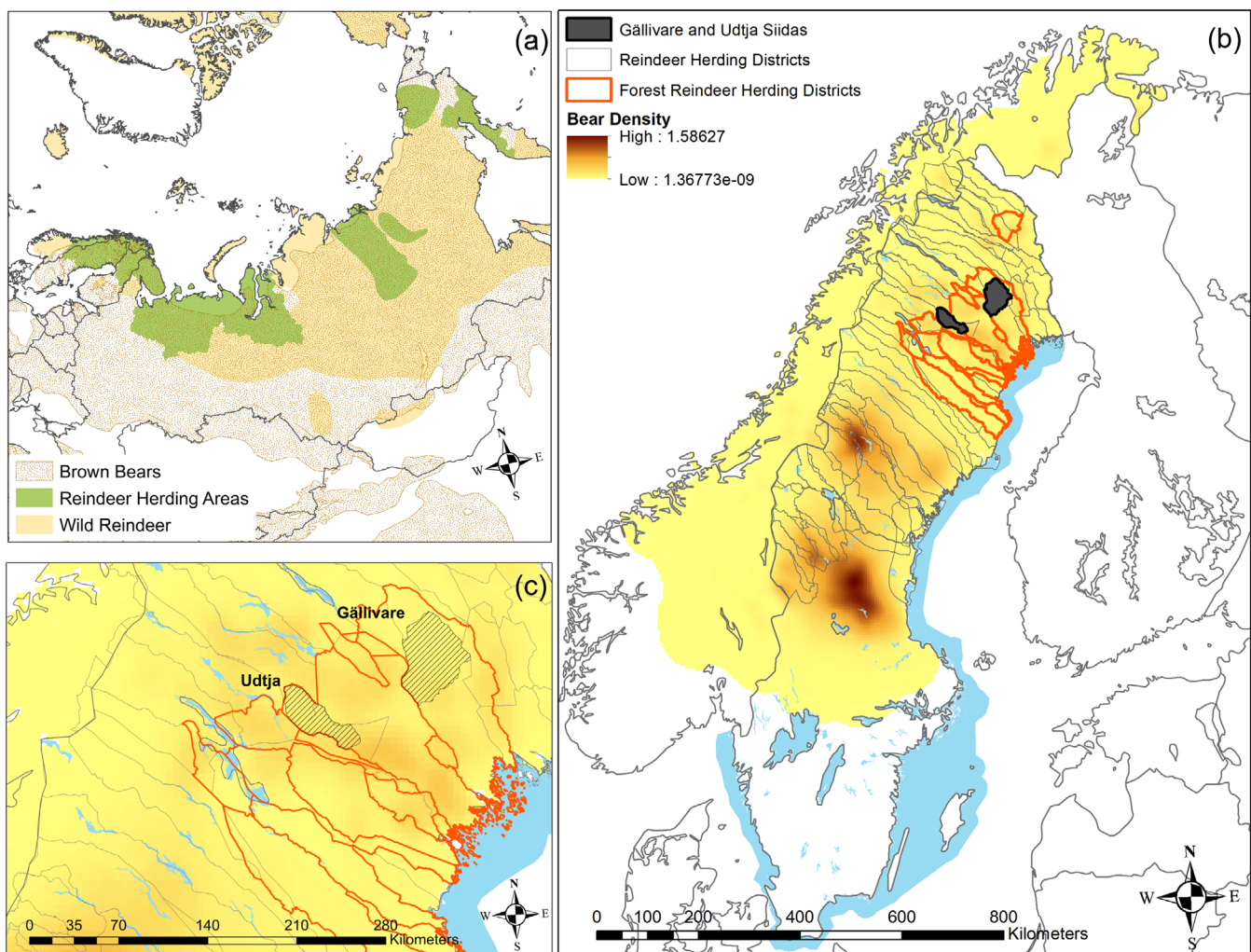


FIGURE 1 The (a) distribution of brown bears (brown dots) and wild reindeer (yellow; www.iucn.org) and 10 major reindeer herding communities in northern Eurasia (green; Uboni et al., 2016), (b) reindeer herding communities in Sweden (gray lines) with forest-based herding communities outlined in orange and the study areas in dark gray, overlaid on bear density (yellow/brown) from the year 2016 (Bischof et al., 2020), and (c) the study area in Norrbotten, Sweden in enlargement. The scale for bear density is the number of bears per 25 km².

between 2014 and 2016 to evaluate the efficacy and economic feasibility of three potential predation mitigation measures: enclosing pregnant female reindeer in corrals during parturition, localized bear lethal management removals, and regional bear license hunting. In collaboration with the Sámi communities, we designed an experiment to evaluate whether calving in corrals increased overall calf survival (Figure 2). We also took advantage of similar data, collected between 2010 and 2012 in the same study area, to compare non-coral-born calf survival between the two study periods. Using previously estimated local bear kill rates (Støen et al., 2022), we also estimated the potential effect of localized bear management removals on subsequent reindeer calf predation. Finally, we estimated the cost:benefit ratio of the different mitigation measures for herding communities, including two different types of lethal management removal (helicopter and camera-trap facilitated removals), to evaluate their economic feasibility. This unique collaborative case study informs both brown bear management and reindeer herding practices in boreal latitudes and may help facilitate coexistence between large carnivores and traditional pastoralist communities elsewhere.

STUDY AREA

There are 51 reindeer herding communities situated in either Arctic alpine (mountain) or subalpine/boreal (forest) habitats in Sweden (Horstkotte et al., 2022; Sköld, 2015). This study was conducted in two Sámi reindeer herding communities, Udtja and Gällivare, which lie in the boreal forest in Norrbotten County, Sweden (Figure 1). This region is dominated by a dense mix of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) with an understory of lichen (*Cladina* sp.), reindeer's primary winter forage, and ericaceous heather (*Ericaceae* sp.). Traditionally, reindeer herders allow their herds to range freely throughout the year, and reindeer give birth on summer calving grounds inside community boundaries, generally between May and beginning of June (Eloranta & Nieminen, 1986; Nieminen et al., 2013). Calving areas within the calving grounds change from year to year based on weather and snow conditions, as calving reindeer are generally restricted to snow-free areas. Pregnant reindeer have one calf per season.

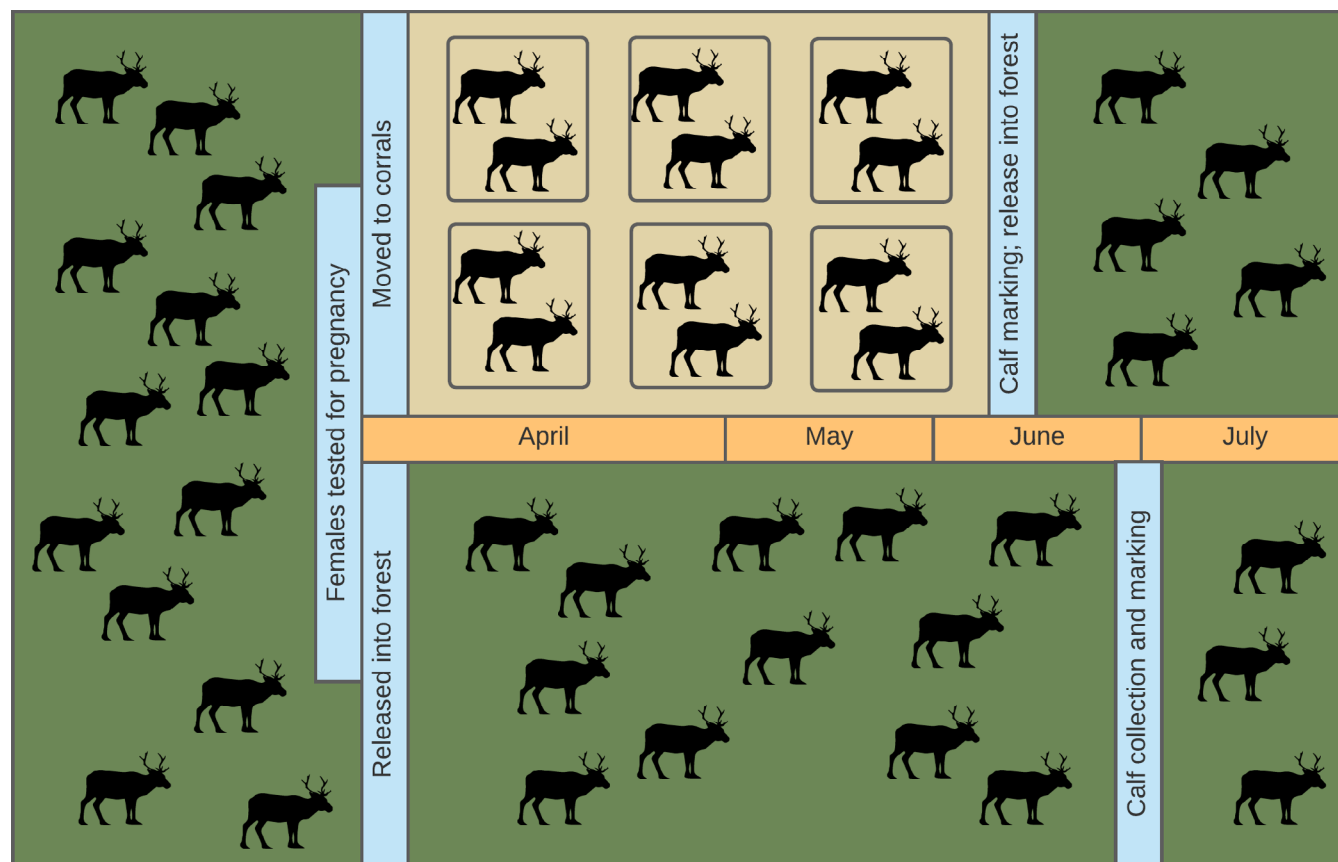


FIGURE 2 The experimental design used to investigate how calving in corrals versus the forest affected reindeer calf survival in the Udtja and Gällivare Sámi herding communities (2014–2016). All females were captured and pregnancy tested. The timeline shows the timing of pregnancy testing (range = 6–15 April), calf marking after birth in the corrals, represented by gray boxes (3–5 June) and in the forest (27 June–6 July) (Appendix S1: Table S1).

Herding communities are divided into several units or “siida/sijte”; siida/sijte (hereafter siida) are the Northern and Southern Sámi words for a reindeer herding group commonly, but not exclusively, formed by a family unit. According to Sámi regulation, the Udtja reindeer herding community occupies 9139 km² (where the winter area is shared with three other communities) and is allowed a maximum of 2800 reindeer in the winter herd, which were divided between two siidas: Udtja and Rödingsträsk. This study was conducted in the Udtja siida, located in the western part of the community (Figure 1), which holds ~1200 females in the winter herd. Reindeer calving generally occurs within ~1280-km² area inside the community boundary (Figure 1). The Gällivare reindeer herding community occupies 8321 km² and is allowed a maximum of 7000 reindeer, which are divided between four siidas: Purnu, Ratukkavaara, Flakaberg, and Muddus. In Gällivare, the study was conducted in the Purnu siida, located in the central part of the community, which holds about 1600 females in winter herds (Figure 1), with reindeer calving occurring within a ~2470-km² area (Figure 1). For simplicity, we hereafter refer to the study areas as Udtja and Gällivare, respectively. Traditionally, herders in both communities cooperatively corral, count, and mark calves in late June/early July, and then divide the reindeer based on ownership in November/December to move them to separate winter grounds or send them to slaughter.

Predators in Sweden include brown bears, which prey on reindeer calves during the parturition period (Nieminen et al., 2013; Sivertsen, 2017; Twynham et al., 2021), lynx and wolverine, which prey on reindeer year-round (Mattisson et al., 2011; Nybakk et al., 2002), red fox (*Vulpes vulpes*; Tveraa et al., 2003), and golden eagle (*Aquila chrysaetos*; Norberg et al., 2006). Wolves also prey on reindeer (Kojola et al., 2004; Nieminen et al., 2013), although lethal management largely restricts their population to outside reindeer herding areas in Sweden (Ordiz et al., 2015; Svensson et al., 2021). Both study siidas overlap the brown bear range (Figure 1), but local lynx and wolverine abundances were low, that is, lynx and wolverine predation were not considered a primary concern by the local herders. Brown bears are legally hunted in Sweden during fall, with hunting quotas set by local administrative units (Bischof et al., 2008).

METHODS

Calf survival

We used a before-after-control-treatment design (Figure 2) to evaluate the effect of corrals on reindeer calf survival.

Between 2014 and 2016, herders rounded up all female reindeer within each siida and field crews tested them for pregnancy. Pregnancy examinations were performed with rectal ultrasound or a combination of rectal ultrasound and palpation (for further details see Paul, 2014). All pregnant females were weighed and then sequentially and alternately marked with uniquely numbered and colored collars and either (a) placed in a corral or (b) released into the open forest calving grounds (Figure 2). Only pregnant females, and eventually their newborn calves, were corralled. Note the experiment was implemented in Gällivare only in 2014 and 2015, and in both Udtja and Gällivare in 2016 (see Appendix S1: Section A).

Corralled reindeer were, in general, provided with supplementary feed in addition to the natural forage within the corral. However, one corral in 2014 in Gällivare with a low ratio of females per hectare (<2) was not provided supplementary feed (Appendix S1: Table S1). The feed rate per day was initially 2.0–2.5 kg per female, which incrementally increased until it reached ~3 kg toward the end of the calving period. Corral fences were 2 m high and covered an area between 12 and 60 ha (Appendix S1: Table S1). The fence boundaries were walked daily by herders to patrol for, and potentially haze away, bears. Corrals were searched daily for deceased reindeer (both calves and females), and carcasses were examined to ascertain the cause of death (e.g., stillbirth, emaciation, disease, etc.). If the cause of death for calves could not be established on-site, the carcass was sent to the National Veterinary Institute (SVA) in Uppsala, Sweden for necropsy. Note that we were unable to locate all the carcasses of calves that died in corrals. Before females and calves were released from the corrals in the beginning of June (Appendix S1: Table S2), all calves were identified in relation to their mother, fit with uniquely numbered ear-tags, sexed, and weighed.

Pregnant female reindeer that were released into the forest calving grounds to give birth were checked for calves during the traditional June/July roundup (Appendix S1: Table S2). During this check, herders attempt to round up all females and calves from the forest calving grounds. However, not all females were found during June/July roundups. The collared females that were successfully rounded up were identified and marked as having a calf present or not. All calves were weighed, classified by sex, and fit with unique ear tags that were linked to their mother's collar.

Due to constraints surrounding the timing of traditional reindeer herding practices, calf survival was measured at different times for females that gave birth in corrals (early June) compared to the forest (late June/early July) (Appendix S1: Table S2), which was an obvious source of potential bias. Importantly, the majority of bear–reindeer

calf predation occurs in May (Støen et al., 2022), after which bears switch to neonate moose calves (Twynham et al., 2021). Nevertheless, we attempted to account for any additional corral-born-calf mortality that may have occurred after release from corrals and before the June/July roundup by fitting a random selection of corral-born calves with mortality transmitters. Mortality signals were checked for via fixed-wing aircraft regularly and, when detected, a crew member located the carcass and assessed the cause and time of death.

We also took advantage of data from a previous study on bear predation in the same Udtja and Purnu siidas (i.e., Udtja and Gällivare) between 2010 and 2012 (Støen et al., 2022) to assess and compare calf survival from that study period. During the 2010–2012 study, all females belonging to the two siidas were similarly tested for pregnancy and weighed during the annual April roundup. All pregnant females were subsequently collared and released to give birth in the forest calving grounds. Finally, all surviving calves were identified in relation to their mother, fit with ear-tags, sexed, and weighed during the traditional June/July roundup.

To evaluate the difference in survival between corral- and forest-born calves, we analyzed how the treatment method (forest/corral) affected the probability that calves survived until the June or June/July roundup. Analyses were conducted in R version 4.0.2 (R Core Team, 2020) using generalized linear mixed models (GLMMs) with a binomial error distribution using the “lmer” package version 1.1-23 (Bates et al., 2015). Year and siida were fit as random intercepts to account for the influence of variation between years and siida on calf survival; these were removed if they did not contribute to model fit, that is, the variance was 0. We also included female weight (range = 47–104 kg) as a control variable (centered and scaled), as the condition of ungulate mothers can affect subsequent calf condition and survival (Ropstad, 2000). Models included a compound symmetric correlation structure and were estimated with adaptive Gaussian quadrature with parameters estimated from maximum likelihood. We removed females who were still pregnant from the survival analysis, as well as females whose weight was not measured for logistical reasons. We also examined calf survival between 2010 and 2012 for the forest-born calves using a similar model structure; we included year as a random effect (siida had 0 variance) and female weight (range = 40–100 kg) as a fixed effect.

Economic feasibility

We evaluated the economic impacts of calving in corrals and local lethal management removals on reindeer

herders by (1) calculating the total costs of materials and labor for each mitigation measure and (2) estimating the net gain/loss per calf saved, that is, per calf that would otherwise have been depredated. To simplify the economic impact assessment, we assumed that all reindeer calves killed by bears would have otherwise survived until fall slaughter. We considered using the total mortality estimates for calves born in corrals as a measure of compensatory mortality, however, mortality could be exacerbated by corralling (e.g., through increased disease transmission via supplementary feeding; Åhman et al., 2018), and may not reflect true compensatory mortality in the wild. We, therefore, exclude potential compensatory mortality from our economic feasibility estimates. We based the value of a reindeer calf on the official compensation value for traffic-killed reindeer calves in Sweden, which is calculated as the weighted average price per kilogram from the previous slaughter season (www.sametinget.se). Although the study was conducted between 2014 and 2016, we used an updated value for 2021 to represent current values; calves were valued at €233 each (1€ [Euro] = US\$1.1).

For the corral mitigation measure, we differentiate between costs for equipment, which are independent of reindeer herd size (e.g., fence rollers or sackcloth), and costs that increase with the number of females and size of the corral (e.g., fencing, feed, and feeding troughs), which are stated as cost per 100 females (see Appendix S1: Section B). We expected the net gain/loss per calf would vary depending on the number of bears in the area and the size of the siida (i.e., the number of reindeer allowed per group). We, therefore, estimated the net gain/loss per saved calf under six different scenarios. Scenarios included small (500 reindeer) and large (5000 reindeer) herding communities overlapping three different bear population sizes: small (9 bears), medium (30 bears), and large (82 bears). Representative small and large herding community sizes are based on personal communication with the Sámi Parliament. Bear population size is based on the range of observed bear populations within the 10 forest-based reindeer calving grounds in Sweden using data from Bischof et al. (2020), and reindeer herding community and calving ground data collected from www.sametinget.se. We selected all forest-based herding community calving grounds in Sweden and estimated the bear population within a 19.7-km buffer (see Appendix S1: Section C) around each area using the 2016 data from Bischof et al. (2020) (Appendix S1: Figure S4, Table S15). We then used the minimum, mean, and maximum observed number of bears across all forest-based herding areas in Sweden (Appendix S1: Table S15) to generate the above biologically representative small, medium, and large bear populations in forest reindeer calving grounds.

As before, we only wanted to consider predatorily active bears in our economic analysis. Thus, we used a conversion factor of 0.45 (the mean proportion of bears found to be predatorily active in 2010/2106; Appendix S1: Table S14) to estimate the proportion of bears that would be potentially predatorily active in small (4), medium (14), and large (37) bear populations (Table 1).

The net gain/loss per saved calf was calculated as

$$g_c = \frac{(N_b \times r_{bp} \times v_c) - (N_f \times c_c) - (N_f \times r_p \times r_{cm} \times v_c)}{(N_b \times r_{bp})}$$

where g_c is the net gain/loss per saved calf (in Euros), N_b is the number of predatorily active bears in the herding group, r_{bp} is the mean bear predation rate (10.2 calves per bear per year; Støen et al., 2022), v_c is the monetary value of a reindeer calf in 2021, N_f is the number of female reindeer in the herding group, r_p is the pregnancy rate among female reindeer, c_c is the cost per female reindeer of corralling, and r_{cm} is the mean mortality rate of reindeer calves born in corrals. “Predatorily active bears” is defined as individual bears within the population that actively prey on reindeer, that is, this excludes females with cubs of the year and dependent cubs (Støen et al., 2022; see Appendix S1: Section C). We included all female reindeer in potential corralling

efforts, as annual pregnancy tests would be unfeasible in most herding communities. We assume that a corral lasts 10 years before it needs to be replaced. Since the corral building is an investment that yields a return for the lifetime of the corral, we analyzed the costs and benefits of all management measures over the entire lifetime of a corral. For this, we use a discount rate of 3% to estimate the net present value of the costs and benefits over the entire period, based on the discussion on appropriate discount rate in Drupp et al. (2018); see Appendix S1: Section B for details. We also calculated the realized cost per corralled female and per saved calf for each study area and year, and report the results in Appendix S1: Section B.

For local management removals and license hunts, we calculated the costs of helicopter-facilitated management removal, camera-trap-facilitated management removal, and regular legal license hunt (i.e., nonmanagement removal). The net gain/loss per saved calf (g_c) was calculated as

$$g_c = \frac{(N_h \times r_{bp} \times v_c) - (N_h \times c_h)}{(N_h \times r_{bp})}$$

where N_h is the number of bears harvested and c_h is the cost of removal per bear. Note that management removals are conducted by local herders, who pay for the cost of the hunt. For helicopter removals, costs were

TABLE 1 Cost/benefit analysis (in Euros; 1€ = US\$1.1) for corralling reindeer during calving season under six scenarios: small (500 reindeer) and large (5000 reindeer) herding communities overlapping small (9 bears), medium (30 bears), and large (82 bears) bear populations.

Variable	Small bear population		Medium bear population		Large bear population	
	Small community	Large community	Small community	Large community	Small community	Large community
N_{bp} (no. bears in population)	9	9	30	30	82	82
N_b (no. predatorily active bears)	4	4	14	14	37	37
r_{bp} (bear predation rate)	10.2	10.2	10.2	10.2	10.2	10.2
v_c (calf value in 2021)	€205	€205	€205	€205	€205	€205
N_f (no. female reindeer)	500	5000	500	5000	500	5000
r_p (female pregnancy rate)	92%	92%	92%	92%	92%	92%
c_c (cost per female of corralling)	(€105)	(€105)	(€105)	(€105)	(€105)	(€105)
r_{cm} (mean corral-born calf mortality rate)	11.6%	11.6%	11.6%	11.6%	11.6%	11.6%
Potential number of calves saved	41	41	138	138	377	377
Gain from calves saved from predation	€8469	€8487	€28,291	€28,291	€77,329	€77,329
Loss from cost of corralling	(€52,500)	(€525,000)	(€52,500)	(€525,000)	(€52,500)	(€525,000)
Loss of calves due to corralling	(€10,937)	(€109,745)	(€10,974)	(€109,745)	(€10,974)	(€109,745)
Total net gain/loss	(€54,968)	(€626,257)	(€35,183)	(€606,453)	€13,855	(€557,415)
g_c (net gain/loss per calf saved from predation)	(€1331)	(€15,126)	(€255)	(€4394)	€37	(€1478)

Note: Values without parentheses are benefits; values in parentheses are costs.

estimated using the price of helicopter capture for research, which is a similar procedure (see Appendix S1: Section B). For camera-trap facilitated removals, we conducted a mini-experiment with camera traps where we measured both cost and success in terms of the number of bear visits per camera (see Appendix S1: Section B). Briefly, camera-trap facilitated removals rely on bait stations (i.e., lure) and game cameras to locate bears. Cameras are triggered by a bear, a picture is sent via text message to the hunter, and the hunter travels to that location and uses dogs to locate and shoot the bear. The cost of licensed hunting was estimated at zero, as they are voluntarily conducted at the hunters' expense. We also looked at trends in the number of bears harvested via management removal and license hunts in our study area using harvest/management data collected between 2010 and 2016. We similarly discounted the costs and benefits for these two measures over a period of 10 years using a 3% discount rate to allow for comparability of the three measures (see Appendix S1: Section B).

RESULTS

Calf survival

Between 2014 and 2016, we placed 1251 marked pregnant females into calving corrals in April (Appendix S1: Table S3). Upon release in early June, we counted 1187 females (64 females were removed from the study; see Appendix S1: Table S3). Of the remaining 1187 females,

1068 had calves, 113 had no calf, and 6 were still pregnant (Appendix S1: Table S3). Across all study areas (2014–2016), an average of 88.4% of corralled females had calves upon release (Appendix S1: Table S3). We identified and ascertained the cause of death for 37 (33%) calves in the corrals (Appendix S1: Table S4); the majority (20) died from emaciation. During the same timeframe, we released 1241 marked pregnant females into the forest to give birth (Appendix S1: Table S5). In total, 1033 (81.9%) of the marked females were rounded up during June/July (Appendix S1: Table S5). Of the forest females that were rounded up, we counted 875 with calves and 158 without (Appendix S1: Table S5). Across all study areas (2014–2016), an average of 83.2% of females rounded up from the forest had calves (Appendix S1: Table S5). After removing females that were (1) still pregnant in June ($N = 6$) or (2) had no recorded weight ($N = 41$), we were left with 1165 marked females in the corral treatment and 1008 control females that ranged freely during the calving and post-calving period for the 2014–2016 study seasons ($N = 2173$).

For the 2014–2016 study period, calf survival was lower for females that gave birth in the forest compared to the corrals ($\beta = -0.62$; 95% CI = -0.89 to -0.35), and increased with adult female weight ($\beta = 0.37$; 95% CI = 0.24 – 0.51 ; Figure 3). At the mean female weight (77 kg), the probability a calf survived was 7.6% higher if it was born in a corral versus the forest (Figure 3). At the minimum observed female weight (47 kg), the probability a calf survived was 14.4% higher if it was born in the

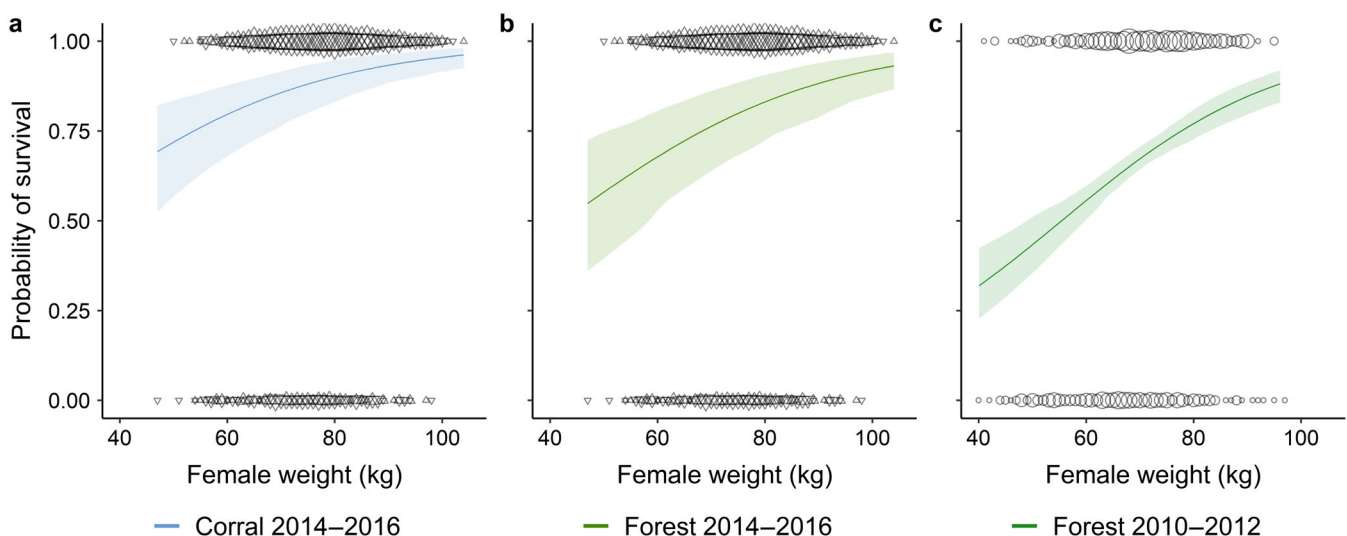


FIGURE 3 The probability a reindeer calf survived until calf marking given that they were born and weaned in (a) corrals (blue) or (b) the forest (green) during the 2014–2016 study, or (c) the forest in the 2010–2012 study. Lines are population-averaged fitted values with associated 95% CIs from respective models (Appendix S1: Table S6). Triangle (pointing up/down = corral/forest) in (a, b) and circle (c) sizes show observed frequencies.

corral (Figure 3). Survival was ~4% and ~6% higher in Gällivare compared to Udtja for corral- and forest-born calves, respectively (Appendix S1: Table S6, Figure S1). We marked a total of 715 corral-born calves (70%) with mortality transmitters (Appendix S1: Table S7). We detected a total of seven dead calves between the release from corrals in early June and the June/July roundup; five died from predation (i.e., bears), one by accident, and one from unknown causes (Appendix S1: Table S7). Overall, additional mortality detected by mortality transmitter-fitted corral-born calves between the June release and the June/July roundup was <1% (Appendix S1: Table S7).

Between 2010 and 2012, 1508 pregnant females were marked in April, and the calf status of 1001 of those females was checked during the June/July roundup (Appendix S1: Table S8). Of the forest females that were recollected, 660 females had calves and 341 females did not (Appendix S1: Table S8). Across all study areas (2010–2012), an average of 66.6% of forest females had calves upon roundup (Appendix S1: Table S8). For the 2010–2012 study period, calf survival also increased with adult female weight ($\beta = 0.49$; 0.35–0.63; Figure 3). However, overall calf survival was lower during the 2010–2012 study season than the 2014–2016 season. At comparable mean (77 kg) and minimum (47 kg) female weights from 2014 to 2016, the probability a calf survived in 2010–2012 was 74.3% and 39.7%, respectively (Figure 3). At the mean and minimum female weights, calf survival in 2010–2012 was, therefore, ~7% and ~15% lower than the comparable survival rate for forest-born calves in 2014–2016, and ~15% and ~30 lower than the survival rate for corral-born calves in 2014–2016 (Figure 3), respectively.

Economic feasibility

Cost-to-benefit ratios of calving in corrals

The rationale for all cost estimates related to calving in corrals is described in Appendix S1: Section C. In summary, the fixed cost for building a calving corral that accommodated 200 females was estimated at €13,300 (€6650/100 females). This included the price of fence rollers, feed, burlap, and other consumables (Appendix S1: Table S9). Variable construction costs were estimated at €7700/100 females (Appendix S1: Table S10). Projected annual costs, including supplementary feeding and corral monitoring, were estimated at €10,350/100 females (Appendix S1: Table S11). Under a 10-year scenario (i.e., corrals are operational for 10 years) and using a 3% discount rate, the annual gross cost for corralling females per year totaled €105/female (Table 1; Appendix S1: Section B). For each scenario, we assumed a static

pregnancy rate (r_p) of 92% (Table 1), which was the mean pregnancy rate during the 2014–2016 study. We also assumed a static mortality for corral-born calves (r_{cm}) of 11.6% (Table 1); compared to calves born in the forest, the observed mean mortality rate in corrals during the study (Table 1; Appendix S1: Table S3).

The breakeven point for corralling mitigation measures was at 0.135 bears/reindeer; ratios below that threshold resulted in a net loss, and above that threshold a net gain (Figure 4). From the six scenarios, our results suggest that corralling females during parturition was only cost-effective for small herding communities with large bear populations (net gain = €37) (Table 1, Figure 4). Corralling females in small herding communities with small bear populations (net loss = €1331) and medium bear populations (net loss = €255), and large herding communities with small (net loss = €15,126), medium (net loss = €4394), and large (net loss = €1478) bear populations, all resulted in a net loss (Table 1, Figure 5). Losses were greatest for larger herding communities and communities that overlapped smaller bear populations. Udtja and Gällivare had a realized net loss every study year between 2014 and 2016, which ranged from €2543 to €5951 per saved calf, or €92 to €235 per corralled female (Appendix S1: Table S12).

Cost-to-benefit ratios of lethal management removal

The rationale for all cost estimates related to management removals is described in detail in Appendix S1: Section B. In summary, the estimated cost for management removals, after factoring in the 3% discount rate over 10 years, was €4393 per harvested bear via helicopter, and ~€2724 per harvested bear via camera-trap facilitated removals. Mean bear predation rates imply that for every bear harvested, herders will gain 10.2 calves at slaughter (Støen et al., 2022). Thus, harvesting one bear via camera-trap-facilitated management removal, would save 10.2 calves from bear predation, resulting in a net loss of €633 per bear, costing €62 per saved calf over a 10-year period (Table 2, Figure 5). Harvesting one bear via helicopter would similarly save 10.2 calves from bear predation, but result in a net loss of €2302 per bear, costing €226 per saved calf over a 10-year period (Table 2, Figure 5). Because costs are fixed for each scenario, removing a greater number of bears would increase calf survival, but the costs per saved calf would remain the same.

Realized management lethal removal rates averaged 1.63 and 0.06 bears shot per year between 2008 and 2016 in Udtja and Gällivare, respectively (Appendix S1: Table S14, Figures S2 and S3). Thus, realized management

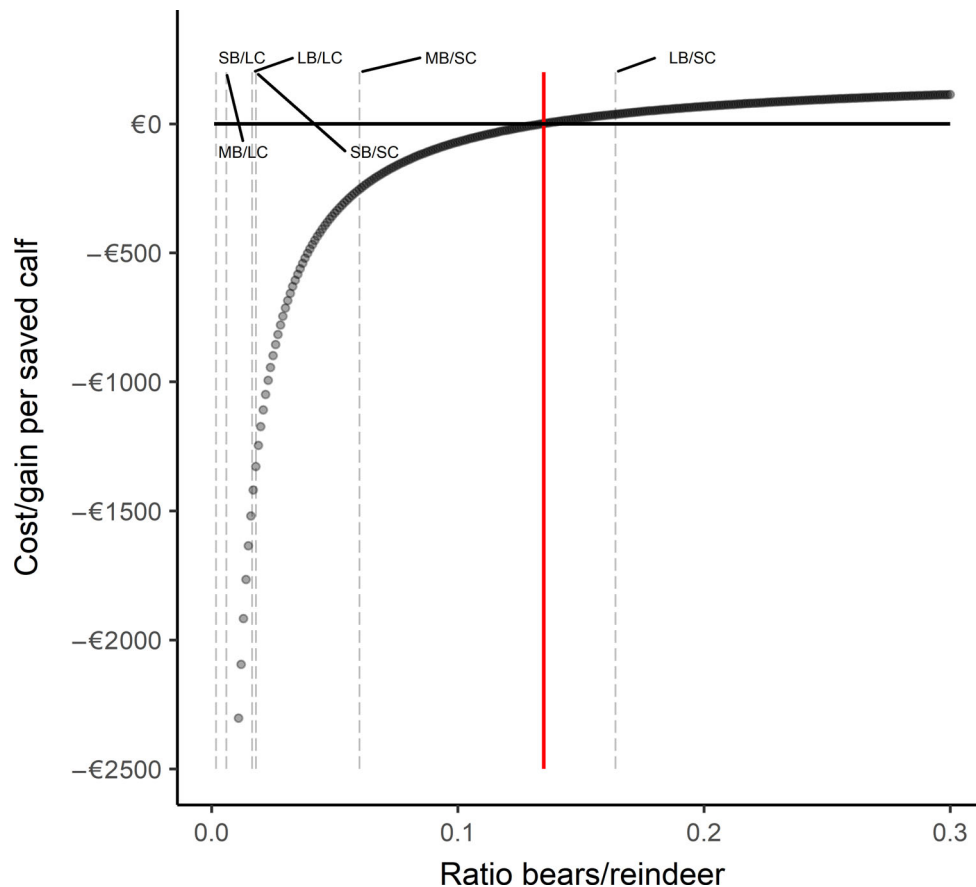


FIGURE 4 The cost/gain per calf saved from predation (in Euros; €1 = US\$1.1) in relation to the ratio of bears per reindeer in a herding community. The red line shows the ratio of bears/reindeer at which point corralling cost would break even (0.135/reindeer or 13.5 bears/100 reindeer). The six different scenarios (dashed lines) are plotted in relation to their bear/reindeer ratio, and include a combination of small (SB), medium (MB), and large (LB) bear populations that overlap with small (SC) and large (LC) reindeer herding communities (e.g., LB/SC represents a large bear population overlapping a small herding community).

removals were relatively minimal and saved between 0.6 and 17.7 calves per year from bear predation. However, between 2014 and 2016, management removals averaged 5.3 and 0.3 bears shot per year in Udtja and Gällivare, respectively, saving between 3.1 and 54.1 calves per year.

Cost-to-benefit ratios of license hunts

The average cost of license hunting was €0 per harvested bear for reindeer herders. At zero cost, license hunting would result in an average net gain of €205 per saved calf over a 10-year period (Table 2, Figure 5). License hunt harvest rates averaged 3.3 and 5.0 bears shot per year between 2008 and 2016 in Udtja and Gällivare, respectively (Appendix S1: Table S14, Figures S2 and S3). Thus, license hunts potentially saved between 33.7 and 51 calves per year from bear predation; this result should be interpreted with caution (see *Discussion*).

DISCUSSION

Our results suggest that the economic impact of bear predation on reindeer herding communities can generally not be mitigated via calving corrals or local lethal management removals. While enclosing females in corrals during parturition resulted in increased calf survival (Figure 3), the cost of implementing this mitigation measure outweighed the financial gain for both our study areas (Appendix S1: Table S12), as well as for almost every scenario we explored (Table 1, Figure 5). The only exception was for small herding communities that overlapped large bear populations, where implementing calving corrals crossed the bear/reindeer ratio efficacy threshold and resulted in a net gain (Table 1, Figures 4 and 5). Similarly, while local lethal management removals could remove multiple predatorily active bears from calving areas, the cost of removal exceeded the potential net gain from saved calves (Table 2, Figure 5). The annual legal license hunt was the most cost-effective

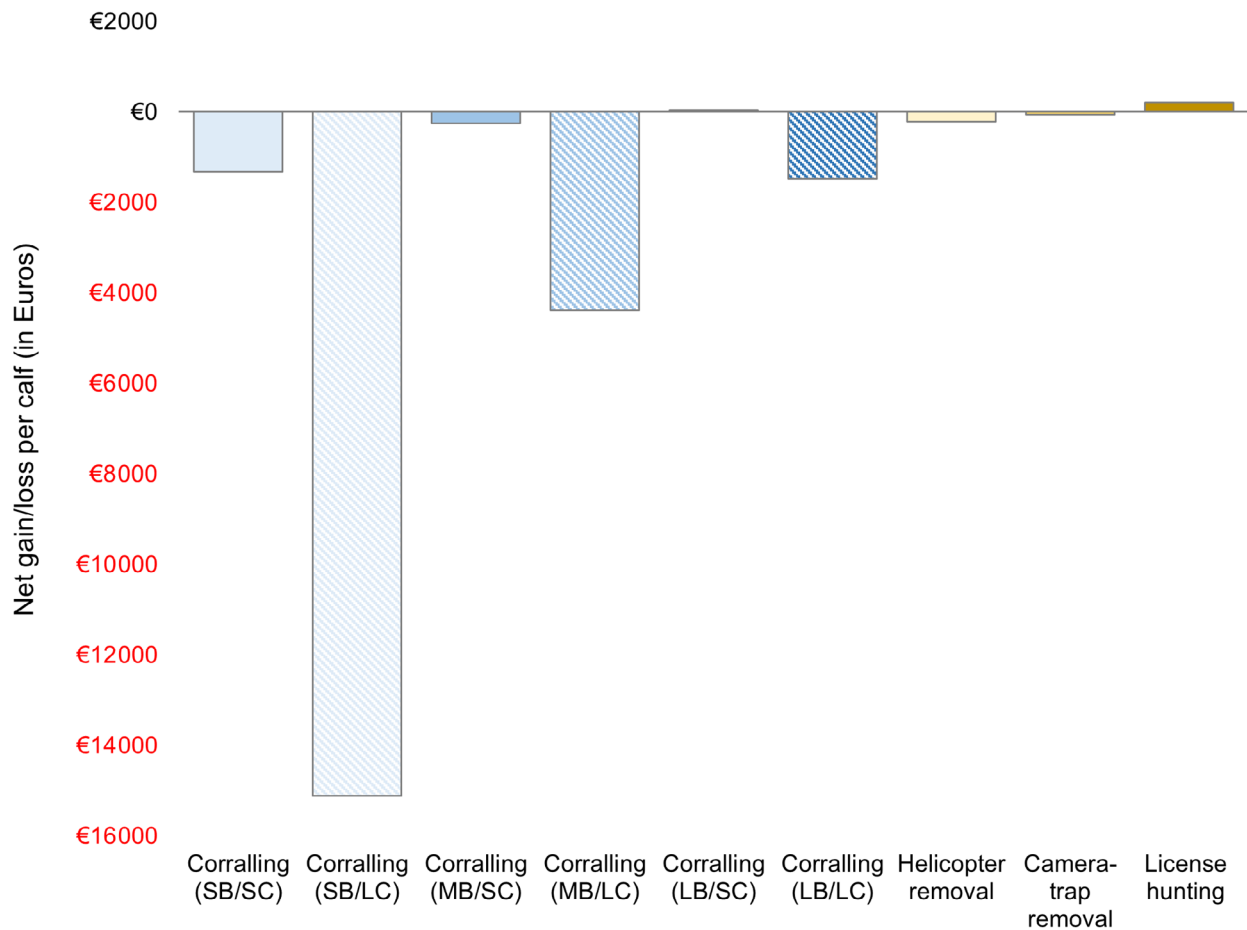


FIGURE 5 Economic feasibility, or the net monetary gain/loss per calf saved in Euros (€1 = US\$1.1), of four different types of bear predation mitigation measures; corraling during calving (blue gradient), helicopter management removals (light yellow), camera-trap-facilitated management removals (medium yellow), and public licensed hunts (brown). The cost of calving in corrals is estimated under six different scenarios that include a combination of small (SB; light blue), medium (MB; medium blue), and large (LB; dark blue) bear populations that overlap with small (SC; solid fill) and large (LC; patterned fill) reindeer herding communities (e.g., LB/SC represents a large bear population overlapping a small herding community; Table 2).

mitigation measure, which had the potential to increase calf survival at no additional cost to herders (Table 2, Figure 5). However, for reasons discussed below, the potential efficacy of license hunting should be interpreted with caution.

Enclosing pregnant female reindeer in corrals during the parturition period mitigated the majority of calf predation and increased overall calf survival. Compared to forest-born calves, corral-born calf survival during the 2014–2016 study was ~7% and 14% higher for calves born to the average and smallest sized females, respectively. However, survival rates of forest-born calves differed between the two study seasons, that is, forest-born calf survival was lower during the 2010–2012 study (Figure 3). Comparing the survival of corral-born calves in 2014–2016 to forest-born calves in 2010–2012, survival increased by ~14% for calves born to average-sized females, and ~30% for calves born to the smallest females (Figure 3). Survival

was likely comparatively higher during the 2014–2016 season because local bear abundance was lower (Appendix S1: Table S16). Decreased bear abundance between study seasons was likely due to relatively high bear harvest rates between 2010 and 2015 (Appendix S1: Figure S2), which included a relatively high offtake of females (Appendix S1: Figure S2) which are a key driver of population dynamics (Frank et al., 2017).

Corrals are an effective livestock depredation mitigation technique against an array of terrestrial mammalian predators (e.g., Ogada et al., 2003; Samelius et al., 2020). Our results correspond with studies from other systems showing that targeted use of corrals during the parturition period can mitigate the depredation of vulnerable young individuals (e.g., Peña-Mondragón et al., 2017; Van Bommel et al., 2007). Alternatively, Tveraa et al. (2003) found that predation may be compensatory to mortalities related to calving corrals for reindeer in northern Norway. However,

TABLE 2 Cost/benefit analysis (in Euros; €1 = US\$1.1) for helicopter and camera-trap-facilitated management removals and license hunts.

Variable	Cost/benefit
Helicopter-facilitated management removal	
v_c (calf value in 2021)	€205
r_{bp} (bear predation rate)	10.2
N_h (no. bears harvested)	1
c_h (cost of hunt per bear)	€4393
Potential no. calves saved	10.2
Gain from calves saved from predation	€2091
Loss from hunting costs	(€4393)
Total net gain/loss	(€2302)
g_c (net gain/loss per calf saved)	(€226)
Camera-trap-facilitated management removal	
v_c (calf value in 2021)	€205
r_{bp} (bear predation rate)	10.2
N_h (no. bears harvested)	1
c_h (cost of hunt per bear)	€2724
Potential no. calves saved	10.2
Gain from calves saved from predation	€2091
Loss from hunting costs	(€2724)
Total net gain/loss	(€633)
g_c (net gain/loss per calf saved)	(€62)
License hunts	
v_c (calf value in 2021)	€205
r_{bp} (bear predation rate)	10.2
N_h (no. bears harvested)	1
c_h (cost of hunt per bear)	€0
Potential no. calves saved	10.2
Gain from calves saved from predation	€2091
Loss from hunting costs	€0
Total net gain/loss	€2091
g_c (net gain/loss per calf saved)	€205

Note: All costs are discounted over a 10-year period using a 3% discount rate (Appendix S1: Table S13). Values without parentheses are benefits; values in parentheses are costs.

the efficacy of calving corrals is likely dependent on the context of the system. For example, the predator guild in the Tveraa et al. (2003) system included only golden eagle, lynx, and wolverine. Bears are a dominant predator of neonate ungulate calves, including neonate reindeer (Adams et al., 1995; Jenkins & Barten, 2005). With other newborn ungulates, the effects of bear predation can be additive to other sources of predator-included mortality (Griffin et al., 2011). Our study suggests that corralling reindeer during the parturition period effectively increases calf survival.

However, while calving corrals effectively abated most bear predation, it ultimately proved an economically ineffective mitigation measure. Had the corralling costs been paid by the communities, rather than the study, both study areas would have incurred net annual losses between ~€16,000 and ~€47,000 (Appendix S1: Table S12). Furthermore, the use of calving corrals resulted in a net financial loss under almost all hypothetical scenarios. The only scenario in which calving corrals might prove economically effective is when there is a high relative density of bears to reindeer (Figure 4), for example, when small herding communities overlap high-density bear areas (Table 1; Appendix S1: Figure S2). However, willingness of herders to invest time, energy, and money to implement the calving corrals is crucial to the success of the mitigation measure. The Sámi Parliament, the Swedish Sámi National Association (SSR), and the Sámi herding communities included in this study all pointed out that corralling and feeding reindeer was inconsistent with traditional Sámi reindeer herding practices, causes extensive wear on the vegetation within the corral, and can have potential negative impacts on reindeer health. Thus, corralling reindeer during parturition is not only economically ineffective, but also culturally inappropriate.

Local lethal management removals were also not an economically viable alternative. While camera-trap-facilitated management removals were the most cost-effective mitigation measure, neither type of management action resulted in a net financial gain (Table 2, Figure 5). The current license hunting program in Sweden was the most economically viable mitigation measure (Table 2, Figure 4). However, license hunting in Sweden takes place during fall (Bischof et al., 2008), which leaves time for the empty niche of harvested bears to be filled by survivors (Frank et al., 2018). Thus, removing one bear during the fall license hunt may result in substantially fewer than 10.2 calves saved, depending on (1) how quickly their niche is filled and (2) whether it is filled by a more or less predatory bear; for example, a non- or low-predatory bear might be replaced by a more predatory bear, because of the individual variation in bears' predatory behavior (Ordiz et al., 2020; Twynham et al., 2021). The fact that large carnivore lethal removal may not necessarily reduce depredation has been shown for other species (e.g., wolves; Fernández-Gil et al., 2016), cautioning that multiple factors influence the expected outcome of such management actions.

Given that these mitigation measures are generally economically ineffective, implementing a fair and functional predation compensation scheme is especially important for reindeer herding communities affected by brown bear predation. For example, Støen et al. (2022) found the siidas in our study areas were annually compensated between €1130 and €1500 by the Swedish

government for bear predation. This reimburses for between ~5 and ~7 calves lost to predation annually, and only covered 3%–6% of the potential financial losses incurred during the corralling experiment (Appendix S1: Table S12). Støen et al. (2022) suggested a revised compensation scheme for Sámi herding communities living in Sweden. Under this new scheme, financial compensation would be based both on the size of the reindeer herding community and the size of the local bear population (Støen et al., 2022), rather than based only on the size of the herding area. This less biased scheme could potentially be implemented with any reindeer herding community worldwide, may help promote coexistence with brown bear populations, and would prevent communities from having to implement non-traditional practices, such as corralling.

Traditional pastoralist systems and large carnivore populations are both under threat worldwide, and their preservation and conservation are key goals as risks associated with climate change and shifting land use alter their environmental and economic landscape (e.g., Dong et al., 2011; Ripple et al., 2014). However, these goals can be antagonistic, as the conservation of large carnivores can negatively impact the traditional livelihood of livestock herders, while management actions can facilitate carnivore population declines (Kaczensky, 1999; Støen et al., 2022). Economically and biologically effective predation mitigation measures are key for promoting coexistence (Pooley et al., 2017; Van Eeden et al., 2018). We suggest that potential mitigation measures should be studied in collaboration with local people, who are then allowed to decide what mitigation measure works best for their local environmental conditions and cultural values (Redpath et al., 2013).

AUTHOR CONTRIBUTIONS

Jens Frank, Ole-Gunnar Støen, Peter Segerström, Lars Thomas Persson, and Rune Stokke conceived of the study. Jens Frank, Ole-Gunnar Støen, Peter Segerström, Birgitta Åhman, Anna Skarin, Torkild Tveraa, Lars Thomas Persson, and Rune Stokke participated in data collection. Aimee Tallian and Bart Immerzeel carried out statistical analysis. Aimee Tallian, Andrés Ordiz, and Ole-Gunnar Støen wrote the manuscript. Jens Frank coordinated the long-term study in Scandinavia. All authors helped draft the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Tallian et al., 2023) are available from Dryad: <https://doi.org/10.5061/dryad.fj6q573zv>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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