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Research article

Effects of large carnivores, hunter harvest, and weather on the mortality of moose calves in a partially migratory population

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Survival of juvenile ungulates represents an important demographic parameter that influences population dynamics within ecosystems. In many ecological systems, the mortality of juvenile ungulates is influenced by various factors, including predation by large carnivores, human hunting activities and weather. While wolves *Canis lupus* are known to prey on moose *Alces alces* throughout all seasons, brown bears *Ursus arctos* primarily engage in predation during early summer, while human harvest primarily occurs in autumn and early winter. Hence, understanding the impacts of predation, harvest, and weather on the survival of juvenile moose is crucial for adaptive population management and the determination of sustainable harvest rates. To investigate the summer and autumn–winter survival of moose calves in relation to carnivore occurrence (wolf presence and bear density), summer habitat productivity, winter severity, human harvest, and migratory behaviour (migratory versus resident), we analysed data collected from 39 GPS-collared female moose in south-central Scandinavia. Our findings revealed significant interannual variation in summer survival rates, with areas with relatively higher bear densities exhibiting calf mortality rates twice as high as those in regions with low bear density. During the autumn–winter period, calf survival was lowest in the presence of wolves and deep snow, and it exhibited a negative correlation with the proportion of clearcuts and young forests within the mother's home range. Additionally, calf survival was negatively correlated with the risk of human hunting, and calves of stationary females displayed ten times higher survival rates compared to migratory individuals. Our study provides valuable insights into the survival of moose calves coexisting with two large carnivores and humans. Improving our understanding of the mechanisms causing calf survival to fluctuate has become increasingly important as many local moose populations in Scandinavia are declining and exposed to expanding predator populations, intense hunting pressure, and other threats associated with climate change.

Keywords: *Alces alces*, *Canis lupus*, predation risk, survival, ungulate, *Ursus arctos*



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Introduction

Survival is a fundamental parameter influencing the demography and population dynamics of ungulates (Gaillard et al. 1998). Variations in survival rates can lead to fluctuations in population density (Gaillard et al. 1998, Loison and Langvatn 1998). Typically, ungulates exhibit a hump-shaped pattern of age-specific survival, with the lowest and most variable rates observed among juveniles, high and stable rates in prime adulthood, and declining rates associated with senescence (Caughley 1966, Gaillard et al. 1998, 2000, Loison et al. 1999). In the absence of human hunting, adult survival rates remain relatively constant from year to year, while juvenile survival rates show high variability (Gaillard et al. 1998). Thus, the temporal variation and unpredictability associated with juvenile survival make it a critical demographic trait affecting population dynamics and trajectories (Houston 1982, Gaillard et al. 1997, 2000, Raithel et al. 2007). Juvenile survival in ungulates is influenced by multiple factors, including predation (Linnell et al. 1995, Swenson et al. 2007), exposure to pathogens (Grobler 1981), access to food resources (Eberhardt 2002, Scornavacca et al. 2016), and weather conditions (Singer et al. 1997, Ericsson et al. 2002, Ciach and Pęksa 2019). Predation often represents the primary source of mortality for neonate ungulates during summer (Linnell et al. 1995, Swenson et al. 2007). The availability of food resources and the nutritional status of individuals strongly influence vital rates in ungulates, and these factors are mostly determined by density-dependent effects associated with the environment (Pettorelli et al. 2005, Toigo et al. 2006). In boreal systems, ungulates frequently utilize clearcuts and young forests early in the growing season due to higher forage density and the presence of high-quality plants (Hjeljord et al. 1990, Boyce et al. 2003, Månsson 2009, Hebblewhite et al. 2008). Plant productivity has been shown to positively affect the survival of both adult and juvenile ungulates (Sims 2017, Hurley et al. 2017).

Winter severity represents an important factor impacting the survival of juvenile ungulates (Loison and Langvatn 1998, Garrott et al. 2003). Snow conditions and cold temperatures restrict movement and increase energy expenditure, potentially making ungulates more vulnerable to predation (Smith et al. 2004, Hebblewhite 2005, Garrott et al. 2008). In ungulate species subjected to human hunting, hunters often constitute the most significant source of mortality for both adults and juveniles (Festa-Bianchet et al. 2003, Apollonio et al. 2010). Hunting can have substantial impacts on demography in harvested populations (Ginsberg and Milner-Gulland 1994, Langvatn and Loison 1999). The effects of large carnivores and hunting on ungulate population dynamics depend on whether predation is additive or compensatory, the specific sex and age classes targeted by these mortality sources, and the cumulative impact of predation-induced mortality in relation to harvest (Bischof et al. 2008). However, the effects of many of these factors remain largely unknown. Therefore, despite the challenges associated with their assessment (Caughley 1977, Eberhardt 1985,

Lebreton et al. 1993), survival rates are crucial parameters for understanding the mechanisms affecting population dynamics and for effectively managing harvested populations (Caughley 1966, Raithel et al. 2007). Thus, investigating changes in survival rates of juvenile ungulates and identifying the factors influencing them is vital for population management, including the estimation of sustainable harvest rates (Porath 1980, Rohm et al. 2007).

Moose *Alces alces* holds significant economic and recreational value across Scandinavia (Storaas et al. 2001, Lavrund et al. 2003, Boman et al. 2011). Over the past two decades, calf/cow ratios and moose densities have generally declined in both areas with and without large carnivores in Sweden (Wikenros et al. 2020, Tallian et al. 2021). In areas with large carnivores, moose face multiple mortality sources that vary in importance over space and time. Brown bear *Ursus arctos* predation is often the primary cause of mortality for neonatal moose in early summer (Swenson et al. 2007). As summer and autumn progress, bear predation declines in significance, while hunting becomes the primary mortality factor for both adult and juvenile moose during early and late autumn (Cederlund and Sand 1991, Lavrund et al. 2003). Wolves *Canis lupus* also pose a significant mortality risk to moose throughout the year, particularly to calves (Sand et al. 2005, 2008). As expected, winter mortality of moose calves in Norway was higher in wolf territories compared to areas lacking wolves (Saether et al. 1996, Sivertsen et al. 2012). The spatial and temporal variations in the presence of hunters and large carnivores underscore the importance of investigating the impact of human-related, abiotic, and biotic factors on moose calf mortality patterns. Given the declining moose densities (Tallian et al. 2021), understanding the factors that influence moose demography, such as calf survival, becomes increasingly important as carnivore populations expand and in the context of climate change, which may lead to increased thermoregulation costs (Murray et al. 2006, Lenarz et al. 2009). This knowledge is essential for providing management strategies that can mitigate the effects of large carnivores and hunting mortality.

In this study, we used position data from 39 GPS-collared female moose in south–central Scandinavia to investigate seasonal calf survival during summer and autumn/winter. We examined the survival probability of calves in relation to the presence of wolves, wolf predation risk, bear density, human harvest and associated hunting risk, habitat productivity, clearcuts and young forests (hereafter referred to as young forests) and snow depth. During summer, we hypothesized that calf survival would be higher in areas with greater productivity and a higher proportion of young forests (*forage opportunity hypotheses*), while it would be lower in the presence of wolves and with increasing bear density (*predation hypotheses*). During autumn–winter, we predicted that calf survival would decrease with increasing harvest and hunting risk and would be lower in the presence of wolves and with higher wolf predation risk (*predation–hunting hypotheses*). We also hypothesized that calf survival would be lower in areas with greater snow depth in the presence

of wolves compared to areas without wolves (*predation × snow hypothesis*). Additionally, we predicted calf survival to be lower in areas with a higher proportion of young forests, which are known to be risky habitats for moose during winter (Gervasi et al. 2013, Ausilio et al. 2022) (*habitat hypothesis*).

Recent studies have shown that migration can influence neonatal ungulate mortality by reducing the risk of predation for females and their calves (White et al. 2014, Berg et al. 2019). Migratory behaviour allows individuals to better utilize delayed green-up at higher altitudes and experience less intraspecific competition by leaving winter concentration areas (Van Moorter et al. 2021). Thus, we tested the hypothesis that calves with migrating mothers would have higher survival rates compared to those with stationary mothers, during both summer and winter (*migration hypothesis*). Lastly, we predicted that calf survival would vary across years due to annual climatic variations that may affect moose forage availability and thermoregulation (*year hypothesis*).

By investigating these factors and their influence on moose calf survival, we aim to contribute to an increased understanding of the underlying factors shaping calf survival, which ultimately affect moose population demography and dynamics.

Material and methods

Study area

The study was carried out along the Swedish–Norwegian border (60°45′–61°35′N, 11°55′–12°55′E) in the Norwegian municipalities of Trysil, Elverum, Våler and Åsnes and the Swedish counties of Värmland and Dalarna (Fig. 1). The topography of the study area exhibits a gradient from higher altitudes in the north to lower altitudes in the south, with approximate elevations ranging from 900 to 400 m a.s.l. (Copernicus Land Monitoring 2018). The northern part of the study area has a continental climate and is dominated by bare mountains, marsh complexes and deep valleys with dense old-growth forests and vast heathlands (Jansson and Antonson 2011). The forest is primarily composed of Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch (*Betula* spp.) (Jansson and Antonson 2011). The mean daily temperature in January and July are –10 and 15°C, respectively. The ground is typically covered with snow from late October to early May, and the vegetation period spans approximately 140–170 days (www.smhi.se; www.senorge.no). Annual precipitation in the area ranges from approx. 600–1000 mm. The southern part of the study area is mostly dominated by Scots pine, Norway spruce and birch forests,

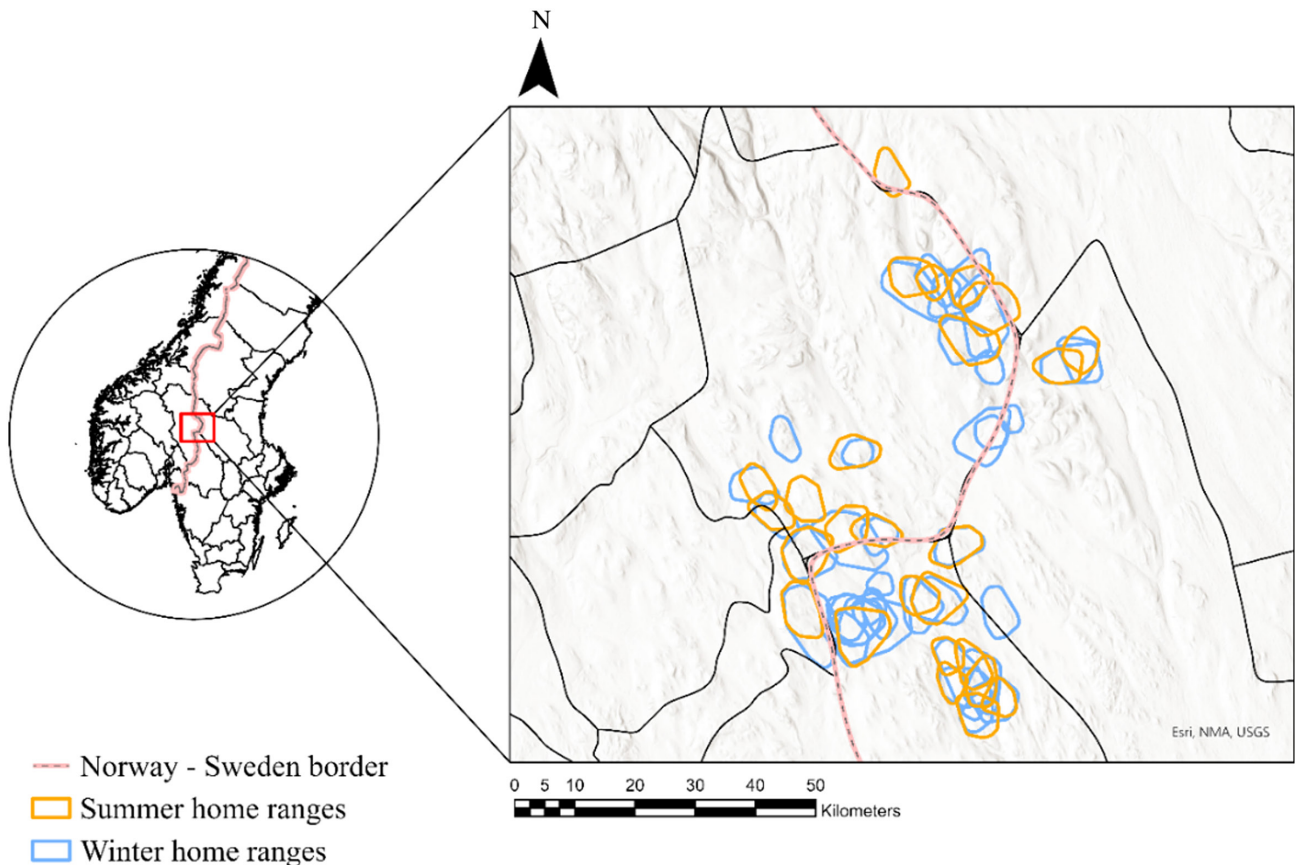


Figure 1. The study was conducted in south–central Scandinavia, along the Swedish–Norwegian border (red square on the left figure). The zoomed-in panel shows the distribution of female moose's winter and summer home ranges.

which are extensively managed for timber and pulp (Yrjölä 2002, Lundmark et al. 2013). The mean temperature in January and July is similar to the northern parts, but snow mostly covers the ground between December and March. Due to intensive silviculture practices, the study area features an extensive network of forest gravel roads. Additionally, the presence of national and regional roads contributes to a mean road density of 0.84 km km⁻² within the study area. Winter moose densities within the study area were estimated using faecal pellet group counts to be 1.25 and 1.27 moose km⁻² in 2018/2019 and 2019/2020 (Zimmermann et al. 2019).

Moose

Moose reproduction

Between February and mid-March (2018–2021), we immobilized 39 adult female moose from a helicopter using a dart gun injecting etorphine and xylazine (Sandegren et al. 1987). The handling protocols adhered to the ethical requirements for research on wild animals in both Sweden (decision C281/6 and C315/6) and Norway (decision id 15370). Each female moose was fitted with a GPS collar (Vectronics Aerospace GmbH, Berlin, Germany) programmed to record a position every 2 h.

During the calving season (May–July), we monitored potential calving events for each collared female using a rolling minimum convex polygon (rMCP) method described by Nicholson et al. (2019). We employed a 12-point moving window to calculate the area of the rMCP within a 24 h period. This timeframe allowed us to include both daytime and nighttime positions and detect changes in movement and space use. Potential parturition events were defined as the earliest date when the mean of overlapping rMCPs remained below 1.7 ha for approximately 72 h. This criterion was based on the behaviour observed by McGraw et al. (2014) in female moose in Minnesota, where extensive movements over large distances occurred just before parturition, followed by a period of minimal movement (presumably just after parturition; 1.72 ± 0.48 ha for 7 days; McGraw et al. 2014). We plotted the overlapping rMCPs for every day from the beginning of May and estimated calving events by identifying spikes in movement prior to periods of little movement (area < 1.7 ha) (Supporting information). To identify the spike in movement before parturition, we set a 25 ha threshold after which a search algorithm was initiated to detect a 72 h period where the average area of the 24 h rMCPs was below 1.7 ha (Nicholson et al. 2019 for details).

Once a calving event was identified, we located the female moose and approached her silently to visually confirm the presence and number of newborn calves. The approach was carried out on foot and using a handheld VHF receiver to locate the female (RX98, Followit, Lindsberg, Sweden). In some cases, drones were employed, flying to the last known GPS position of the female moose and hovering over the area searching for the moose. We waited a minimum of two days and a maximum of seven days from the assumed calving event before each approach. This interval allowed time for

the females to bond with their calves, reducing the risk of calf abandonment. Additionally, it enabled us to collect calf survival data within the first few days after parturition, when calf mortality is typically high.

Once we had visual contact with the female moose, we waited until we had visual confirmation of the number of calves present. In cases where the reproductive status of a female was uncertain during the initial approach, a second approach was conducted 2–7 days later to gather additional information. Females that did not exhibit movement behavior indicating calving were approached between the end of June and mid-July to confirm the absence of calf/calves. We are aware that this method does not determine calving success with absolute certainty, since neonates could have died just after birth and prior to surveys; nonetheless, it represents a reasonably unbiased method to measure the relative production of calves in early summer. Throughout the study, there were only two instances where female moose displayed calving behaviour, but subsequent field checks revealed no presence of calves.

Within one month prior to the onset of the hunting season, each female moose was re-approached to count the number of calves again using the same procedure as in early summer. The hunting season in Norway starts 25 September, whereas it differs within the Swedish part of the study area, starting either in the beginning of September or on the second Monday of October. Accordingly, our approach timing was strategically planned to coincide with the hunting initiation in each respective area, ensuring that the estimates remained unaffected by the onset of hunting activities. Lastly, a final verification of the number of calves accompanying each female was performed before natal dispersal, specifically in April of the following year. This procedure, encompassing calf-checks after birth, prior to hunting, and prior to dispersal, was carried out for the study years 2019–2020, 2020–2021 and 2021–2022.

Moose migratory behaviour and home ranges

To classify the migratory strategies of each female moose, we employed the net squared displacement method (NSD) (Bunnefeld et al. 2011, Singh et al. 2016, Sand et al. 2022). This approach enables the differentiation of various movement strategies, such as migration and residency (Bunnefeld et al. 2011, Börger and Fryxell 2012, Singh et al. 2016), by analysing the displacement patterns of individual animals using non-linear mixed effects models (Singh et al. 2016). The NSD method characterizes migration as a double sigmoid or s-shaped function, which repeats within a year and involves the animal returning to its departure location (Singh et al. 2016).

We used GPS positions to estimate seasonal home ranges for each female moose using 95% minimum convex polygons (MCP). The MCPs were calculated separately for the summer (1 May–31 August; mean = 39 km², range = 15–88 km²) and autumn-winter (1 September until 30 April; mean = 42 km², range = 13–100 km²) periods with the *amt* package in R (www.r-project.org, Signer et al. 2019). Using the start and end date of migration (based on NSD), we excluded GPS positions during migration from our MCP analysis.

Calf survival

Harvest density

We used harvest data from both Norway and Sweden at the moose management area level (Ålgdata 2022; see Wikenros et al. 2020 for details regarding the moose management systems in Norway and Sweden). We calculated harvest density as the number of harvested moose per km² (range=0.11–0.44 moose km⁻²) and extracted the average harvest density within the autumn–winter home range for each female moose.

Large carnivores

Wolves

Wolves belonging to four packs, all having cross border territories along the Swedish–Norwegian border, were located on snow, and immobilized by darting from helicopter (Sand et al. 2006, Arnemo and Evans 2017). Handling protocols fulfilled the ethical requirements for research on wild animals in Sweden (decision C281/6 and C315/6) and Norway (The Norwegian Food Safety Authority, decision id 15370). The collars were programmed to acquire one position every 4 h. We created 95% minimum convex polygons (MCPs) using GPS positions from the scent-marking adult breeders to represent the territory of each wolf pack during summer (May–August) and autumn–winter (September–April) with the package ‘amt’ in R (www.r-project.org, Signer et al. 2019). In cases where multiple adult wolves were collared within a wolf pack during our study period, we prioritized data from the individual with the most extensive collar operation during the specific time interval (referred to as the ‘main individual’). For periods when location data from the main individual were unavailable, we supplemented the dataset with relocations from the other collared adult. We checked for overlap between moose and wolf home ranges during both summer and autumn–winter and categorized each moose home range to be overlapping (entirely or partially) or not overlapping with the wolf home range (0 = no overlap; 1 = overlap), depending on whether they were inside or outside a wolf territory.

Bears

To estimate bear density within the study area, we used density raster maps provided by Bischof et al. (2020). These maps provided estimates of bear density as the number of bears per square kilometer. By overlaying the bear density raster maps with the summer home ranges of each female moose, we extracted the average bear density for each moose’s respective summer home range.

Environmental covariates

We obtained data on young forests from the Corine Land Cover (CLC) inventory (Copernicus Land Monitoring 2018). The inventory defines young forests as thickets, clear-felled areas and young broad-leaved and coniferous forest (Copernicus Land Monitoring 2018). Using this inventory, we calculated the proportion of each female moose’s home

range covered by young forests for each season (summer and autumn/winter) and year (mean = 15 ± 7 ; range = 0–36%).

We used cumulative average winter snow depth from October to March of each study year as a proxy for winter severity. The data was obtained from the Norwegian Water Resources and Energy Directorate (NVE, Senorge 2022) (for more information on the interpolation method used see Saloranta 2012). For each female moose home range in autumn–winter in each year we then extracted average snow depth.

Normalized Difference Vegetation Index (NDVI) is a measure of photosynthetic activity at landscape scales that is often used to as a proxy for plant productivity and nutritional status (Petorelli et al. 2011). We obtained data on NDVI from Copernicus Global Land Service (300 m resolution raster) and used weekly NDVI cell values to calculate the mean cumulative summer NDVI for each moose home range (mean = 0.73 ± 0.08 ; range = 0.53–0.86).

Hunting and wolf predation risk metrics

We used previously estimated relative risks of human hunting and wolf predation for moose in our study area, based on locations of wolf-killed and hunter-killed moose during autumn–winter (September–April; Ausilio et al. 2022). Ausilio et al. (2022) modelled hunting and wolf predation risk separately using logistic regressions with the relative probability of a location being a kill site or a random location as a function of different landscape features (distance to bogs, young forests, main and secondary roads, elevation, building density and terrain ruggedness). The estimates represent the odds ratio (relative risk) of being killed by wolves or hunters (hereafter, relative hunting risk and relative wolf predation risk). The odds ratios for each given location within the study area were then plotted as raster layers (25 × 25 m). For more details on the methods used to estimate wolf predation risk and human hunting risk, Ausilio et al. (2022). We extracted the odds ratio of hunting and wolf predation risk for a subset (n = 31 females) of moose home ranges that overlapped with the risk maps from Ausilio et al. (2022).

Survival analyses

To investigate the factors influencing calf survival during summer and autumn–winter, we used Cox Proportional-Hazard models. These models allowed us to analyse the probability of survival (0 = survived; 1 = died) while considering the repeated checks of individual moose by including moose ID as a covariate. For each season, we initially constructed a full model that included all predictors and interactions based on our hypotheses. To refine the models, we employed step-wise backwards selection, eliminating interactions with $p > 0.10$ and individual predictors with $p > 0.05$.

The summer model included the additive and linear effects of the following predictors: year (three-level factor), wolf presence, bear density, proportion of young forests, migratory behaviour of the mother (migratory versus stationary) and NDVI.

The autumn–winter model included the additive and linear effects of year (three-level factor), harvest density, wolf presence, snow depth, proportion of clear-cuts/young forests and the migratory behaviour. We included the interaction between wolf presence and snow depth to test whether calf survival was lower with deeper snow in the presence of wolves compared to the absence of wolves.

Lastly, we used a subset of female moose to test the effect of hunting and wolf predation risk on autumn–winter calf survival. This supplementary analysis allowed us to evaluate whether the mortality risk metric developed by [Ausilio et al. \(2022\)](#) correlates with calf survival, but also to account for smaller spatial-scale variation in hunting risk compared to overall harvest density, which might be too coarse to detect changes in survival at the individual-level. For this subset of the data, we assumed that calf survival was a function of the additive and linear effects of hunting risk, wolf predation risk and year (three-level factor). All continuous variables were scaled prior to analysis to have mean=0 and standard deviation=1. We could not use all female moose for this analysis because we lacked data about wolf predation risk for 2021/2022, hence why we selected only a subset of moose overlapping in time with our previously estimated metric of wolf predation risk ([Ausilio et al. 2022](#)).

Results

Across our three-year study period, we obtained data from 39 female moose producing a total of 77 calves. The survival

rates of calves from birth to dispersal were 58% for the 2019/2020 season, 42% for the 2020/2021 season, and 52% for the 2021/2022 season.

Summer survival

The best model explaining variation in the survival probability of calves during summer included bear density ($\beta=0.79$, $\exp^\beta=2.21$, $SE=0.34$) and year ($\beta_{2020}=3.38$, $\exp^\beta_{2020}=29.38$, $SE_{2020}=1.24$; $\beta_{2021}=2.94$, $\exp^\beta_{2021}=19.00$, $SE_{2021}=1.23$; Supporting information for model selection), with the probability of survival decreasing with increasing bear density ([Fig. 2](#)). Summer calf survival varied significantly between years, with survival being highest in 2019/2020 (92%), followed by 2021/2022 (69%) and 2020/2021 (58%) ([Table 1](#)).

Autumn–winter survival

The best model explaining variation in the survival probability of calves during autumn–winter included the following covariates: wolf presence ($\beta=-6.63$, $\exp^\beta=0.001$, $SE=0.2.40$), snow depth ($\beta=-0.13$, $\exp^\beta=0.87$, $SE=0.04$), the interaction *wolf* × *snow* ($\beta=0.22$, $\exp^\beta=1.25$, $SE=0.08$), proportion of young forests ($\beta=0.12$, $\exp^\beta=1.13$, $SE=0.05$), and the migratory behaviour of the mother ($\beta=2.28$, $\exp^\beta=9.81$, $SE=0.91$; Supporting information for model selection). Calf mortality did not vary between years: 37, 36 and 30% of all calves died during autumn–winters 2019/2020, 2020/2021 and 2021/2022, respectively ([Table 1](#)).

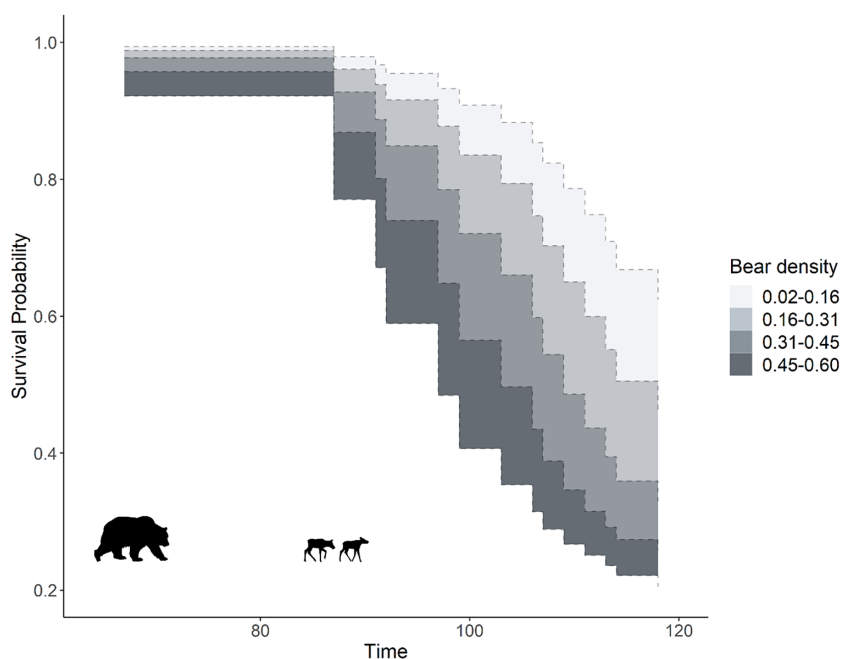


Figure 2. Predicted summer survival probability of moose calves in relation to bear density in south–central Scandinavia. Time represents the number of days since the first field check for each moose. Calf survival was estimated with field checks on GPS-collared female moose after suspected parturition. Bear density was obtained from the raster maps produced by [Bischof et al. \(2020\)](#).

Table 1. Summary table showing the total number of female moose equipped with GPS collars, the number of females that gave birth, the number of females that gave birth to twins, the total number of calves born and the overall summer and winter calf mortality (%) for three years.

Summer	2019/2020	2020/2021	2021/2022
Total number of females	26	27	32
Females that gave birth	22	21	26
Females with twins	2	3	3
Number of calves born	24	24	29
Calf mortality	8%	31%	42%
Autumn–winter	2019/2020	2020/2021	2021/2022
Females with calves	21	12	20
Number of calves	22	14	20
Calf mortality	37%	36%	30%
Annual survival	14/24	10/24	15/29

The interaction *wolf* × *snow* was significant, indicating that in the presence of wolves, snow depth decreased the probability of survival (Fig. 3). However, the probability of calf survival was higher with increasing snow depth in the absence of wolves (Fig. 3). The probability of survival was negatively correlated to the proportion of young forests present within the mother's home range. Harvest density was not related to autumn–winter calf survival, but survival probability was higher for calves of stationary females compared to calves of migrating females (Fig. 4).

The separate analyses on a subset of female moose showed that calf survival was negatively correlated to hunting risk (Fig. 5) but was not significantly related to wolf predation risk (Supporting information).

Discussion

In this study, we found that calf survival during both summer and winter was influenced by several factors including the presence of predators, landscape and climatic features, human activities such as hunting, and behavioural traits such as the migratory behaviour of the mother. Specifically, we observed that summer calf survival decreased with increasing bear density and varied significantly between years, giving support to one of the two *predation hypotheses* and to the *year hypothesis*. During the summer season, brown bears are one of the main predators of moose calves. Previous research has shown that moose calves can constitute a significant portion, ranging from 36 to 44% of the

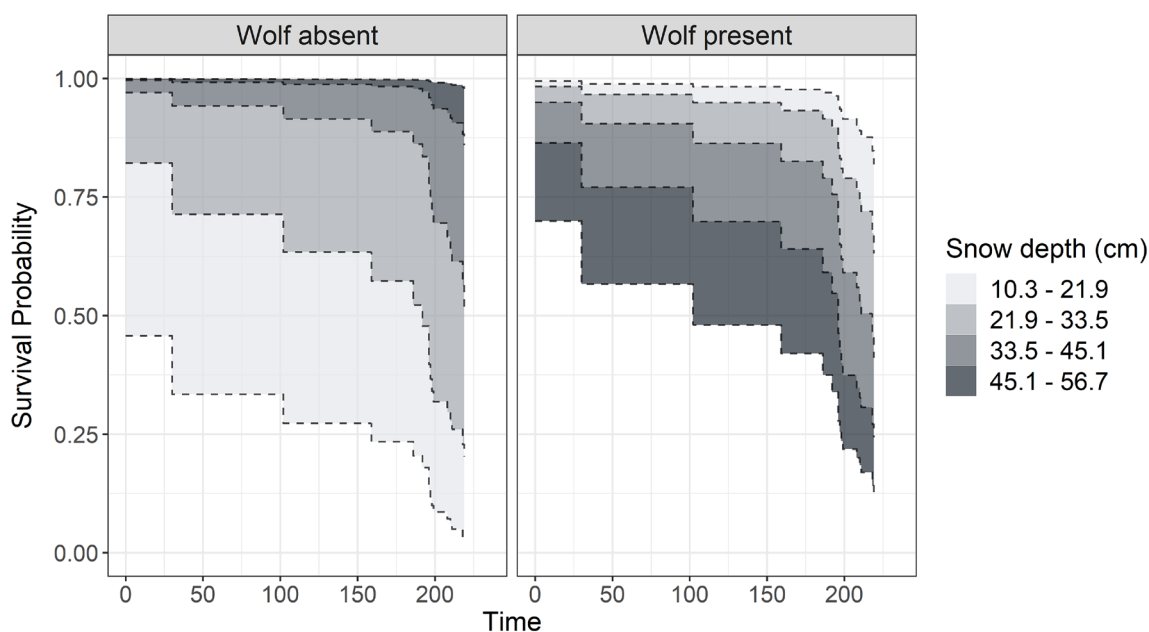


Figure 3. Predicted autumn–winter survival probability of moose calves in relation to wolf presence and snow depth (included as an interaction term in the model) in south-central Scandinavia. Moose calf survival was estimated with field checks on GPS-collared female moose after summer (September–October) and at the end of winter (April of the following year). Wolf presence was estimated using GPS-collared wolves and data on snow depth was obtained from the Norwegian Water Resources and Energy Directorate.

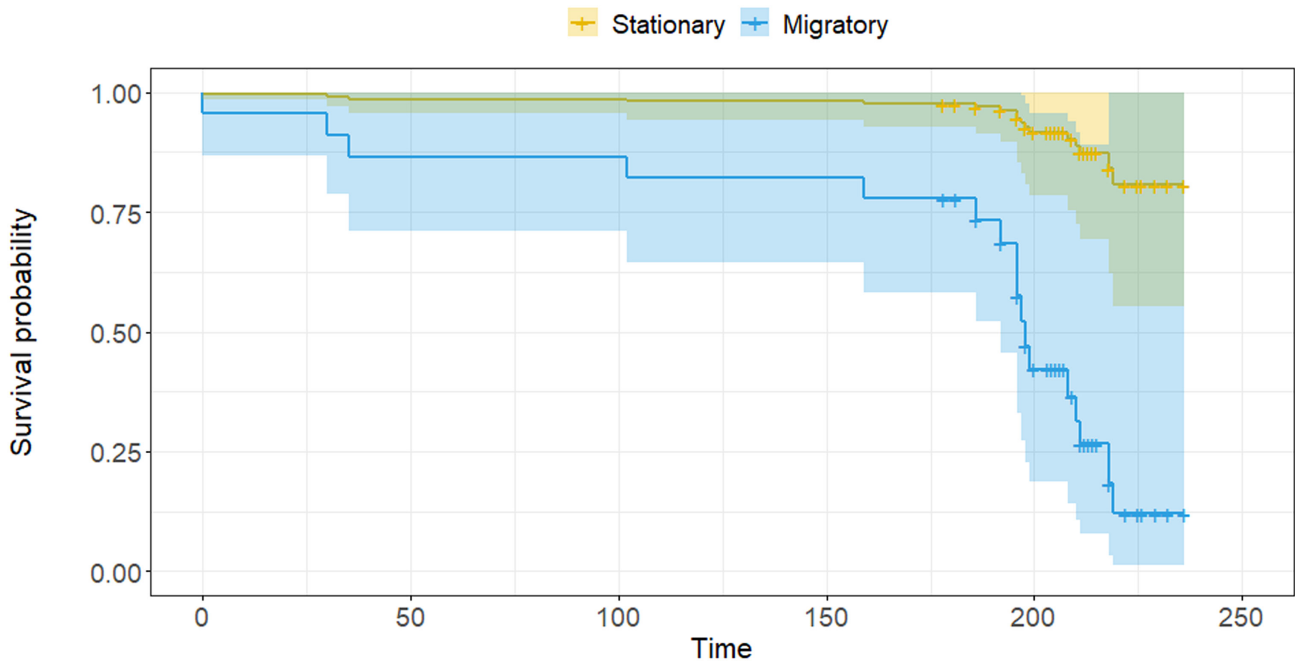


Figure 4. Predicted autumn–winter survival probability of moose calves with migratory versus stationary mothers in south–central Scandinavia. Calf survival was investigated by performing field checks on GPS-collared female moose and their calves. The behavioural behaviour of the mother (migratory or stationary) was estimated using net squared displacement.

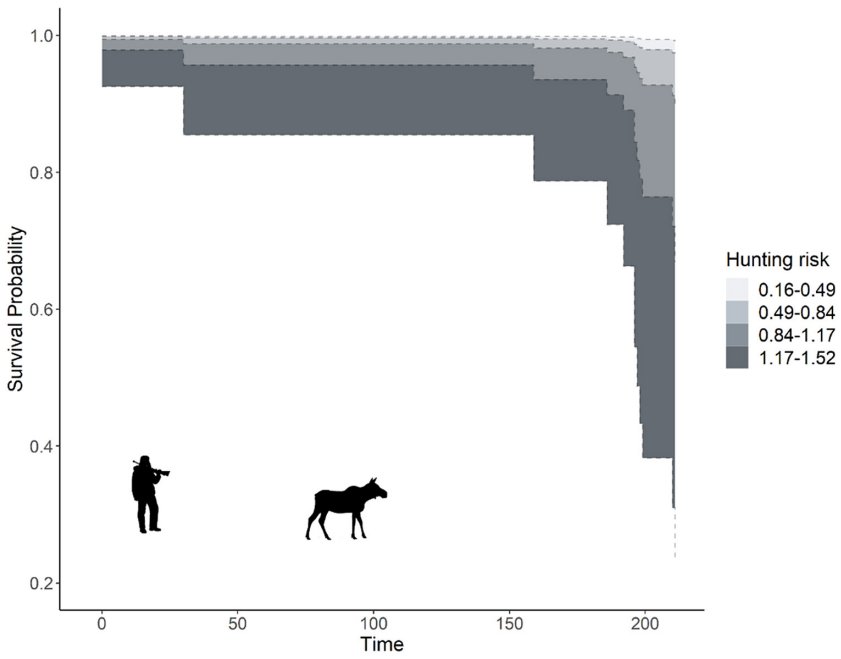


Figure 5. Predicted autumn–winter survival probability of moose calves in relation to hunting risk (expressed as odds ratios) by humans in south–central Scandinavia. Odds ratio can be interpreted as relative hunting risk, where a value of 1.5 indicates a kill probability 1.5 times greater than average. Autumn–winter moose calf survival was estimated with field checks on GPS-collared female moose after summer (September–October) and at the end of winter (April of the following year). Hunting risk was obtained from previous research from the same study area (Ausilio et al. 2022 for further details on how hunting risk was estimated).

total energy content in the diet of brown bears (Opseth 1998). In south–central Sweden, studies estimated a predation rate of 26% for moose calves by brown bears, with individual female bears killing an average of 6.8 calves per year (Swenson et al. 2007). The majority (92%) of brown bear predation on moose calves occurs when the calves are less than one month old (Swenson et al. 2007, Rauset et al. 2012). Our study revealed that the risk of calf mortality is more than twice as high in areas with high bear density compared to areas with low bear density. These findings align with a previous study that found a negative association between bear density and calf/cow ratio (i.e. the number of observed calves per female moose in autumn) in Sweden (Tallian et al. 2021). The lower summer survival rates and decreased autumn calf/cow ratios observed with increasing bear density likely reflect the impact of bear predation on neonate moose.

While we do not have information on cause-specific mortality for each moose calf included in the study, we were able to confirm at least two documented bear predation events during the first study year: one in the northernmost part of the study area, where a pair of twin calves were killed by bears, and one in the easternmost part where the female moose and her calf were observed being followed by a female bear and her two yearling cubs, and the calf was not seen again the following day. Overall, these findings highlight the significant influence of bear predation on the survival of moose calves during the summer season.

In ungulates, the survival of adult females is a crucial driver of population growth, but calf survival can account for up to 75% of the variation in population growth rates (Gaillard et al. 2000, Raithel et al. 2007). Our study supports the notion that bear predation on moose neonates is likely an influential factor driving population dynamics of moose (Swenson et al. 2007, Rauset et al. 2012, Tallian et al. 2021). This is likely to become even more relevant in the future as the brown bear population has been expanding in their southern range (Kindberg 2010, Kindberg et al. 2011) and now overlaps with the core areas of the wolf population.

In Scandinavia, wolves are important predators of newborn moose calves, which make up approximately 90% of wolf kills during the summer season (Sand et al. 2008, Tallian et al. 2017). Surprisingly, we did not detect a relationship between wolf presence and summer calf survival. The lack of such an association might be related to the spatial location of the collared female moose and wolf space use and behaviour during denning time. During the summer season, breeding wolves exhibit more restricted space use compared to winter, focusing their activities around the den area where they care for their pups (Fritts and Mech 1981, Jedrzejewski et al. 2001, Walton et al. 2001, Zimmermann et al. 2019). During the denning period, Scandinavian female and male wolves had a mean attendance at the den site of 68 and 70%, respectively (Alfred en 2006). Consequently, the likelihood of a moose calf being killed by wolves may vary within wolf territories, with higher predation risk closer to the den site compared to farther away.

In our study, we characterized wolf presence based on whether a moose home range was inside or outside a wolf home range. By using this broad classification, we might have overlooked the spatial variation in predation risk within wolf home ranges. This could have resulted in a failure to detect a correlation between wolf presence and calf survival, which may have been influenced by a bias introduced by the sampling of collared females. In other words, our data might have included an overrepresentation of collared female moose that utilized areas with low wolf activity during the summer season.

We offer several potential ad hoc explanations for the lack of support for our *forage opportunity hypotheses* (habitat productivity and proportion of young forests) in our analysis of summer survival. Previous studies have indicated that during the summer season, the composition of moose home ranges tends to resemble the overall landscape, suggesting that moose utilize a greater variety of habitats compared to winter (Hjeljord et al. 1990, Nikula et al. 2004). This may indicate that although clearcuts and young forests are important habitats for moose, the more homogenous distribution of high-quality, nutritional plant forage during summer allows moose to find optimal feeding patches in different habitats, also explaining why productivity was unrelated to calf mortality. Moreover, Nicholson et al. (2014) found that during summer, females with calves had lower selection strength for young forests and tended to select older forests, which may also explain why we did not find a correlation between calf mortality and the proportion of young forests.

The observed annual variation in summer survival of neonates is likely an effect of differing weather features. Neonate growth and survival can be negatively affected by hot and dry summers due to nutritional constraints (Cook et al. 2004), but also by the environmental conditions experienced by their mothers in the preceding summer and during pregnancy in the preceding winter and spring (Forchhammer et al. 2001, Bastille-Rousseau et al. 2016, Eacker et al. 2016).

During autumn–winter, calf survival exhibited a negative association with increasing snow depth in the presence of wolves (*predation × snow hypothesis*) and an increasing proportion of young forests in the mother's home range (*habitat hypothesis*). In addition, calf survival was higher for stationary moose calves compared to migratory calves, contrary to our initial prediction (*migration hypothesis*). Deep snow can hinder the movement of both wolves and moose, but since the former have a lighter foot loading, they can often travel on top of the snow crust (Peterson 1974). Hence, deeper snow generally increases the vulnerability of moose to predation and therefore increases the hunting success of wolves (Kolenosky 1972, Peterson and Allen 1974, Haber 1977) and kill rate (Nelson and Mech 1986, Huggard 1993, Post et al. 1999). Contrary to expected, we found that deeper snow was positively correlated with calf survival the absence of wolves. Although surprising, this unexpected result may be confounded by spatial variations in snow depth within our study area: in the northernmost part, where wolves are absent, snow depth averaged 45 cm, whereas average snow

depth in the central and southern parts (where wolves are present) was only 22 cm. Thus, the absence of wolves and the generally higher snow depths in the northernmost region might be contributing to the observed positive relationship between calf survival and snow depth.

As food resources become scarcer during winter, moose commonly aggregate in young forest plantations to feed (Gundersen 2003), with Scots pine being the quantitatively most important food source (Månsson 2007). In our study, we observed a negative relationship between calf survival and the proportion of young forests during autumn–winter. This finding supports the notion that clearcuts and young forests represent riskier habitats for moose, both in terms of predation by wolves (Gervasi et al. 2013, Ausilio et al. 2022) and hunting by humans (Ausilio et al. 2022).

Game harvesting has become the leading cause of mortality in many ungulate species (Allendorf et al. 2008, Darimont et al. 2015), with moose calves accounting for about 40% of total harvest of moose in Scandinavia (www.algdata.se; www.ssb.no). We did not find a relationship between harvest density and moose calf survival, but we found a significant negative correlation between hunting risk and autumn–winter survival: calves exposed to high hunting risk had twice the risk of mortality compared to calves exposed to low hunting risk. The lack of a relationship between harvest density and survival is most likely a result of the spatial scale at which both harvest statistics and harvest density were calculated, which is the moose management unit (MMU). Moose management units are larger (average \pm SE = 1830 \pm 140 km², Wikenros et al. (2020)) than an average moose home range (68 \pm 7 km²), which means that one MMU can include several hundreds of moose home ranges. Moose management units are in turn made up by many hunting teams. Unfortunately, harvest density at the hunting team level was not available, so we decided to average harvest density at the MMU-level, which may be a too coarse spatial scale to identify a significant correlation between harvest density and calf survival. Hunting risk was, on the other hand, estimated at a much finer spatial scale (hunting team level, Ausilio et al. 2022) and was negatively correlated to calf survival, providing support for the hunting part of our *predation-hunting hypothesis*.

In our study area, the moose population is partially migratory, with some individuals moving between high-altitude summer ranges and low-altitude winter ranges. Migration is usually the product of balancing the costs and benefits of remaining in a range all year-round or moving to new areas. We found that the migratory behaviour of females was unrelated to summer calf survival, while during autumn–winter, migratory females were associated with a lower probability of calf survival compared to stationary ones. This outcome was opposite to our *migration hypothesis*. Adopting a stationary tactic offers several benefits, including the advantage of year-round range familiarity, reduced density-dependent competition (Marthysen 2005), as well as circumventing the risk of being obstructed or constrained from reaching seasonal ranges (Kokko and Sutherland

2001, Holdo et al. 2011, Sawyer et al. 2013). Therefore, a possible explanation as to why migratory moose in our study had higher calf mortality might be that they experienced increased density-dependent competition when entering winter ranges, or due to lower site-familiarity selected sub-optimal habitats. Additionally, another possible reason is that migratory moose in our study area moved from summer ranges, that were often located in Norway where the hunting season stopped already in December, to winter ranges in Sweden where the hunting season continued to February.

Both the wolf and brown bear populations have increased during the last decades and expanded their geographical distribution in Scandinavia (Kindberg et al. 2011, Liberg et al. 2012), and in many areas these two predators have overlapping ranges (Kindberg et al. 2011). A future scenario likely to arise is therefore increased predation pressure on moose, which will intensify the competition with human hunters for this shared prey (Jonzén et al. 2013). In areas where wolves and bears coexist with human hunters, the additive effects of two large carnivores and human harvest will most likely result in greatly reduced calf survival, which may influence population dynamics. Increased predation pressure may also have the potential to influence the dynamics of partial migration, as documented by Berg et al. (2023) in a partially migratory elk population in Canada. There, the higher survival of juveniles of migrant elk contributed to the shift in migratory behaviour observed in the population (Berg et al. 2023), most likely due to differential predation by brown bears between migratory tactics as well as additive effects of predation. How predation affects the dynamics of partial migration is practically unknown in Scandinavia but could have important implications for forestry and hunting practices. Our findings about calf survival in a partially migratory moose population provide a good foundation for further studies investigating the factors influencing migratory behaviours adopted by ungulates in multi-predator systems.

To ensure a sustainable harvest of the moose population, calf survival is a crucial demographic parameter to take into consideration, especially with the ongoing decline in the Scandinavian moose population. The coexistence of wolves, brown bears, and human hunters presents challenges that can lead to reduced calf survival, ultimately influencing population dynamics. To ensure a balanced and sustainable harvest of the moose population, comprehensive management strategies need to account for the intricate interplay between predation, hunting, climate and migratory behaviours. This is important not only for moose, but also other species of large herbivores that are exposed to mortality from multiple predators and hunters. Population declines of large herbivore species have been observed in Europe (Loison et al. 2003, Putman et al. 2011) and North America (Murray et al. 2006, DeCesare et al. 2014). Changes in population size and dynamics of large herbivores can have significant implications for ecosystems, as these animals affect not only vegetation structure and heterogeneity but are also crucial drivers of ecosystem processes (Hobbs 1996, Ripple et al. 2016).

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Permits – Between February and mid-March (2018–2021), we immobilized 39 adult female moose from a helicopter using a dart gun injecting etorphine and xylazine (Sandegren et al. 1987). The handling protocols adhered to the ethical requirements for research on wild animals in both Sweden (decision C281/6 and C315/6) and Norway (decision id 15370). Wolves belonging to four packs, all having cross border territories along the Swedish–Norwegian border, were located on snow, and immobilized by darting from helicopter (Sand et al. 2006, Arnemo and Evans 2017). Handling protocols fulfilled the ethical requirements for research on wild animals in Sweden (decision C281/6 and C315/6) and Norway (The Norwegian Food Safety Authority, decision id 15370).

Author contributions

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Data availability statement

Data are available from the Dataverse Digital Repository at this link: <https://doi.org/10.18710/YJRJXT> (Ausilio et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Alfredéen, A. C. 2006. Denning behaviour and movement pattern during summer of wolves *Canis lupus* on the Scandinavian Peninsula. – PhD thesis, Sveriges Lantbruksuniversitet. Institutionen för Naturvårdsbiologi, Sweden.
- Älgdata 2022. – <https://www.kartverket.no>.
- Allendorf, F. W., England, P. R., Luikart, G., Ritchie, P. A. and Ryman, N. 2008. Genetic effects of harvest on wild animal populations. – *Trends Ecol. Evol.* 23: 327–337.
- Apollonio, M., Andersen, R. and Putman, R. 2010. European ungulates and their management in the 21st century. – Cambridge Univ. Press.
- Arnemo, J. M. and Evans, A. L. 2017. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. – Inland Norway Univ. of Applied Sciences, doi:10.13140/RG.2.2.30359.37286.
- Ausilio, G., Wikenros, C., Sand, H., Wabakken, P., Eriksen, A. and Zimmermann, B. 2022. Environmental and anthropogenic features mediate risk from human hunters and wolves for moose. – *Ecosphere* 13: e4323.
- Ausilio, G., Sand, H., Wikenros, C., Aronsson, M., Milleret, C., Nordli, K., Wabakken, P., Eriksen, A., Persson, J., Maartmann, E. and Zimmermann, B. 2023. Data from: Effects of large carnivores, hunter harvest, and weather on the mortality of moose calves in a partially migratory population. – Dataverse Repository, <https://doi.org/10.18710/YJRJXT>.
- Bastille-Rousseau, G., Schaefer, J. A., Lewis, K. P., Mumma, M. A., Ellington, E. H., Rayl, N. D., Mahoney, S. P., Pouliot, D. and Murray, D. L. 2016. Phase-dependent climate–predator interactions explain three decades of variation in neonatal caribou survival. – *J. Anim. Ecol.* 85: 445–456.
- Berg, J. E., Hebblewhite, M., Clair, C. C. and Merrill, E. H. 2019. Prevalence and mechanisms of partial migration in ungulates. – *Front. Ecol. Evol.* 7: 325.
- Berg, J. E., Eacker, D. R., Hebblewhite, M. and Merrill, E. H. 2023. Summer elk calf survival in a partially migratory population. – *J. Wildl. Manage.* 87: e22330.
- Bischof, R., Mysterud, A. and Swenson, J. E. 2008. Should hunting mortality mimic the patterns of natural mortality? – *Biol. Lett.* 4: 307–310.
- Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., de Valpine, P., Turek, D., Royle, J. A., Gimenez, O., Flagstad, Ø., Åkesson, M., Svensson, L., Brøseth, H. and Kindberg, J. 2020. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. – *Proc. Natl Acad. Sci. USA* 117: 30531–30538.
- Boman, M., Mattsson, L., Ericsson, G. and Kriström, B. 2011. Moose hunting values in Sweden now and two decades ago: the

- Swedish hunters revisited. – *Environ. Resour. Econ.* 50: 515–530.
- Börger, L. and Fryxell, J. 2012. Quantifying individual differences in dispersal using net squared displacement. – *Dispersal Ecol. Evol.* 30: 222–230.
- Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., Turner, M. G., Fryxell, J. and Turchin, P. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. – *Ecoscience* 10: 421–431.
- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J. and Ericsson, G. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. – *J. Anim. Ecol.* 80: 466–476.
- Caughley, G. 1966. Mortality patterns in mammals. – *Ecology* 47: 906–918.
- Caughley, G. 1977. Analysis of vertebrate populations. – The Blackburn Press.
- Cederlund, G. and Sand, H. 1991. Population dynamics and yield of a moose population without predators. – *Alces J. Devoted Biol. Manage. Moose* 27: 31–40.
- Ciach, M. and Pęksa, Ł. 2019. Human-induced environmental changes influence habitat use by an ungulate over the long term. – *Curr. Zool.* 65: 129–137.
- Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D. and Irwin, L. L. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. – *Wildl. Monogr.* 155: 1–61.
- Copernicus Land Monitoring, Service 2018. – Cover, Corine Land.
- Darimont, C. T., Fox, C. H., Bryan, H. M. and Reimchen, T. E. 2015. The unique ecology of human predators. – *Science* 349: 858–860.
- DeCesare, N. J., Smucker, T. D., Garrott, R. A. and Gude, J. A. 2014. Moose status and management in Montana. – *Alces J. Devoted Biol. Manage. Moose* 50: 35–51.
- Eacker, D. R., Hebblewhite, M., Proffitt, K. M., Jimenez, B. S., Mitchell, M. S. and Robinson, H. S. 2016. Annual elk calf survival in a multiple carnivore system. – *J. Wildl. Manage.* 80: 1345–1359.
- Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. – *J. Wildl. Manage.* 49: 997–1012.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. – *Ecology* 83: 2841–2854.
- Ericsson, G., Ball, J. P. and Danell, K. 2002. Body mass of moose calves along an altitudinal gradient. – *J. Wildl. Manage.* 80: 91–97.
- Festa-Bianchet, M., Gaillard, J. M. and Côté, S. D. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. – *J. Anim. Ecol.* 72: 640–649.
- Forchhammer, M. C., Clutton-Brock, T. H., Lindström, J. and Albon, S. D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. – *J. Anim. Ecol.* 70: 721–729.
- Fritts, S. H. and Mech, L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. – *Wildl. Monogr.* 80: 3–79.
- Gaillard, J. M., Boutin, J. M., Delorme, D., Van Laere, G., Duncan, P. and Lebreton, J. D. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. – *Oecologia* 112: 502–513.
- Gaillard, J.-M., Festa-Bianchet, M. and Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. – *Trends Ecol. Evol.* 13: 58–63.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annu. Rev. Ecol. Syst.* 31: 367–393.
- Garrott, R. A., Eberhardt, L. L., White, P. J. and Rotella, J. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. – *Can. J. Zool.* 81: 33–45.
- Garrott, R. A., White, P. J., Becker, M. S. and Gower, C. N. 2008. Apparent competition and regulation in a wolf-ungulate system: interactions of life history characteristics, climate, and landscape attributes. – *Terr. Ecol.* 3: 519–540.
- Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P. and Linnell, J. D. C. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. – *Ecol. Appl.* 23: 1722–1734.
- Ginsberg, J. R. and Milner-Gulland, E. J. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. – *Conserv. Biol.* 8: 157–166.
- Grobler, J. H. 1981. Parasites and mortality of sable *Hippotragus niger niger* (Harris, 1838) in the Matopos, Zimbabwe. – *Koedoe* 24: 119–123.
- Gundersen, H. 2003. Vehicle collisions and wolf predation: challenges in the management of a migrating moose population in southeast Norway. – PhD thesis, Univ. of Oslo, Norway.
- Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. – Univ. of British Columbia, Canada.
- Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. – *J. Anim. Ecol.* 74: 226–233.
- Hebblewhite, M., Merrill, E. and McDermid, G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. – *Ecol. Monogr.* 78: 141–166.
- Hjeljord, O., Hövik, N. and Pedersen, H. B. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. – *Ecography* 13: 281–292.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. – *J. Wildl. Manage.* 60: 695–713.
- Holdo, R. M., Fryxell, J. M., Sinclair, A. R., Dobson, A. and Holt, R. D. 2011. Predicted impact of barriers to migration on the Serengeti wildebeest population. – *PLoS one* 6: e16370.
- Houston, D. B. 1982. The northern Yellowstone elk. – Macmillan.
- Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. – *J. Wildl. Manage.* 57: 382–388.
- Hurley, M. A., Hebblewhite, M., Lukacs, P. M., Nowak, J. J., Gaillard, J. M. and Bonenfant, C. 2017. Regional-scale models for predicting overwinter survival of juvenile ungulates. – *J. Wildl. Manage.* 81: 364–378.
- Jansson, U. and Antonson, H. 2011. Jordbruk och skogsbruk i Sverige sedan år 1900–studier av de Areella näringarnas geografi och historia: Kungl. – Skogs-och Lantbruksakademien.
- Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. and Okarma, H. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. – *Can. J. Zool.* 79: 1993–2004.
- Jonzén, N., Sand, H., Wabakken, P., Swenson, J. E., Kindberg, J., Liberg, O. and Chapron, G. 2013. Sharing the bounty – adjusting harvest to predator return in the Scandinavian human-wolf-bear-moose system. – *Ecol. Modell.* 265: 140–148.
- Kindberg, J. 2010. Monitoring and management of the Swedish brown bear (*Ursus arctos*) population.
- Kindberg, J., Swenson, J. E., Ericsson, G., Bellemain, E., Miquel, C. and Taberlet, P. 2011. Estimating population size and trends

- of the Swedish brown bear *Ursus arctos* population. – *Wildl. Biol.* 17: 114–123.
- Kokko, H., Sutherland, W. J. and Johnstone, R. A. 2001. The logic of territory choice: implications for conservation and sources ink dynamics. – *Am. Nat.* 157: 459–463.
- Kolenosky, G. B. 1972. Wolf predation on wintering deer in east-central Ontario. – *J. Wildl. Manage.* 36: 357–369.
- Langvatn, R. and Loison, A. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. – *Wildl. Biol.* 5: 213–223.
- Lavsund, S., Nygrén, T. and Solberg, E. 2003. Status of moose populations and challenges to moose management in Fennoscandia. – *Alces J. Devoted Biol. Manage. Moose* 39: 109–130.
- Lebreton, J. D., Pradel, R. and Clobert, J. 1993. The statistical analysis of survival in animal populations. – *Trends Ecol. Evol.* 8: 91–95.
- Lenarz, M. S., Nelson, M. E., Schrage, M. W. and Edwards, A. J. 2009. Temperature mediated moose survival in northeastern Minnesota. – *J. Wildl. Manage.* 73: 503–510.
- Liberg, O., Aronson, Å., Sand, H., Wabakken, P., Maartmann, E., Svensson, L. and Åkesson, M. 2012. Monitoring of wolves in Scandinavia. – *Hystix. Ital. J. Mammal.*, doi:10.4404/hystrix-23.1-4670.
- Linnell, J. D. C., Aanes, R. and Andersen, R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. – *Wildl. Biol.* 1: 209–223.
- Loison, A. and Langvatn, R. 1998. Short-and long-term effects of winter and spring weather on growth and survival of red deer in Norway. – *Oecologia* 116: 489–500.
- Loison, A., Festa-Bianchet, M., Gaillard, J. M., Jorgenson, J. T. and Jullien, J. M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. – *Ecology* 80: 2539–2554.
- Loison, A., Toïgo, C. and Gaillard, J.-M. 2003. Large herbivores in European alpine ecosystems: current status and challenges for the future. – In: Nagy, L. et al. (eds), *Alpine biodiversity in Europe*. Springer Science and Business Media, pp. 351–366.
- Lundmark, H., Josefsson, T. and Östlund, L. 2013. The history of clear-cutting in northern Sweden – driving forces and myths in boreal silviculture. – *Forest Ecol. Manage.* 307: 112–122.
- Matthysen E. 2005. Density-dependent dispersal in birds and mammals. – *Ecography* 28: 403–416.
- Månsson, J. 2009. Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. – *Ecography* 32: 601–612.
- Månsson, J., Kalén, C., Kjellander, P., Andrén, H. and Smith, H. 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. – *Scand. J. Forest Res.* 22: 407–414.
- McGraw, A. M., Terry, J. and Moen, R. 2014. Pre-parturition movement patterns and birth site characteristics of moose in northeast Minnesota. – *Alces J. Devoted Biol. Manage. Moose* 50: 93–103.
- Murray, D. L., Cox, E. W., Ballard, W. B., Whitlaw, H. A., Lenarz, M. S., Custer, T. W., Barnett, T. and Fuller, T. K. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. – *Wildl. Monogr.* 166: 1–30.
- Nelson, M. E. and Mech, L. D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. – *J. Wildl. Manage.* 50: 471–474.
- Nicholson, K. L., Milleret, C., Månsson, J. and Sand, H. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. – *Oecologia* 176: 69–80.
- Nicholson, K. L., Warren, M. J., Rostan, C., Månsson, J., Paragi, T. F. and Sand, H. 2019. Using fine-scale movement patterns to infer ungulate parturition. – *Ecol. Indic.* 101: 22–30.
- Nikula, A., Heikkinen, S. and Helle, E. 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. – *Wildl. Biol.* 10: 121–135.
- Opseth, O. 1998. Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern taiga zone in Sweden. – MSc thesis, Norwegian Univ. of Science and Technology, Norway.
- Peterson, R. O. 1974. Wolf ecology and prey relationships on Isle Royale. – Purdue Univ., USA.
- Peterson, R. O. and Allen, D. L. 1974. Snow conditions as a parameter in moose-wolf relationships. – *Nat. Can.* 101: 481–492.
- Pettorelli, N., Weladji, R. B., Holand, O., Mysterud, A., Breie, H. and Stenseth, N. C. 2005. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. – *Biol. Lett.* 1: 24–26.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M. and Kausrud, K. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. – *Clim. Res.* 46: 15–27.
- Porath, W. R. 1980. Fawn mortality estimates in farmland deer range. White-tailed deer population management in the north central states. – In: Hine, R. L. and Nehls, S. (Eds), *Proceedings of the 1979 symposium of the north central section of the wildlife society*, Urbana, Illinois, USA, pp.55–63.
- Post, E., Peterson, R. O., Stenseth, N. C. and McLaren, B. E. 1999. Ecosystem consequences of wolf behavioural response to climate. – *Nature* 401: 905–907.
- Putman, R., Apollonio, M. and Andersen, R. (eds) 2011. *Ungulate management in Europe: problems and practices*. – Cambridge Univ. Press.
- Raithel, J. D., Kauffman, M. J. and Pletscher, D. H. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. – *J. Wildl. Manage.* 71: 795–803.
- Rauset, G. R., Kindberg, J. and Swenson, J. E. 2012. Modeling female brown bear kill rates on moose calves using global positioning satellite data. – *J. Wildl. Manage.* 76: 1597–1606.
- Ripple, W. J. et al. 2016. Saving the world's terrestrial megafauna. – *BioScience* 66: 807–812.
- Rohm, J. H., Nielsen, C. K. and Woolf, A. 2007. Survival of white-tailed deer fawns in southern Illinois. – *J. Wildl. Manage.* 71: 851–860.
- Saether, B. E., Andersen, R., Hjeljord, O. and Heim, M. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. – *Ecology* 77: 1493–1500.
- Saloranta, T. M. 2012. Simulating snow maps for Norway: description and statistical evaluation of the seNorge snow model. – *Cryosphere* 6: 1323–1337.
- Sand, H., Zimmermann, B., Wabakken, P., Andrén, H. and Pedersen, H. C. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. – *Wildl. Soc. Bull.* 33: 914–925.
- Sand, H., Wikenros, C., Wabakken, P. and Liberg, O. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? – *Proc. R. Soc. B* 273: 1421–1427.
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, O., Pedersen, H. C. and Liberg, O. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? – *Oecologia* 156: 53–64.

- Sand, H., Zimmermann, B., Berg, E., Bramorska, B., Eriksen, A., Wikenros, C., Ausilio, G., Miltz, C., Niccolai, L. and Wabakken, P. 2022. Vandringsmönster hos GPS-försedda älgar i GRENSEVILT-konsekvenser för förvaltningen. – Swedish Univ. of Agricultural Sciences, Grimsö, Sweden.
- Sandegren, F., Pettersson, L., Ahlqvist, P. and Roeken, B. O. 1987. Immobilization of moose in Sweden [etorphine-xylazine]. – Swedish Wildlife Research (Sweden).
- Sawyer, H., Kauffman, M. J., Middleton, A. D., Morrison, T. A., Nielson, R. M. and Wyckoff, T. B. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. – *J. Appl. Ecol.* 50: 68–78.
- Scornavacca, D., Lovari, S., Corza, A., Bernardini, S., Brunetti, C., Pietrocini, V. and Ferretti, F. 2016. Pasture quality affects juvenile survival through reduced maternal care in a mountain-dwelling ungulate. – *Ethology* 122: 807–817.
- Senorge 2022. – <https://www.kartverket.no>.
- Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – *Ecol. Evol.* 9: 880–890.
- Sims, S. A. 2017. Effects of changing environments on survival of a widely distributed ungulate. All Graduate Theses and Dissertations, Spring 1920 to Summer 2023. – <https://digitalcommons.usu.edu/etd/5947>
- Singer, F. J., Harting, A., Symonds, K. K. and Coughenour, M. B. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. – *J. Wildl. Manage.* 61: 12–25.
- Singh, N. J., Allen, A. M. and Ericsson, G. 2016. Quantifying migration behaviour using net squared displacement approach: clarifications and caveats. – *PLoS One* 11: e0149594.
- Sivertsen, T. R., Mysterud, A. and Gundersen, H. 2012. Moose (*Alces alces*) calf survival rates in the presence of wolves (*Canis lupus*) in southeast Norway. – *Eur. J. Wildl. Res.* 58: 863–868.
- Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S. and Evans, S. B. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. – *J. Wildl. Manage.* 68: 153–166.
- Storaas, T., Gundersen, H., Henriksen, H. and Andreassen, H. 2001. The economic value of moose in Norway – a review. – *Alces J. Devoted Biol. Manage. Moose* 37: 97–107.
- Swenson, J. E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Söderberg, A., Wallin, K. and Cederlund, G. 2007. Predation on moose calves by European brown bears. – *J. Wildl. Manage.* 71: 1993–1997.
- Tallian, A., Ordiz, A., Metz, M. C., Milleret, C., Wikenros, C., Smith, D. W., ... and Sand, H. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. – *Proc. R. Soc. B* 284: 20162368.
- Tallian, A., Ordiz, A., Zimmermann, B., Sand, H., Wikenros, C., Wabakken, P., Bergqvist, G. and Kindberg, J. 2021. The return of large carnivores: using hunter observation data to understand the role of predators on ungulate populations. – *Global Ecol. Conserv.* 27: e01587.
- Toïgo, C., Gaillard, J. M., Van Laere, G., Hewison, M. and Morellet, N. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. – *Ecography* 29: 301–308.
- Van Moorter, B., Singh, N. J., Rolandsen, C. M., Solberg, E. J., Dettki, H., Pusenius, J., Månsson, J., Sand, H., Milner, J. M., Roer, O., Tallian, A., Neumann, W., Ericsson, G. and Mysterud, A. 2021. Seasonal release from competition explains partial migration in European moose. – *Oikos* 130: 1548–1561.
- Walton, L. R., Cluff, H. D., Paquet, P. C. and Ramsay, M. A. 2001. Movement patterns of barren-ground wolves in the central Canadian Arctic. – *J. Mammal.* 82: 867–876.
- White, K. S., Barten, N. L., Crouse, S. and Crouse, J. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. – *Ecology* 95: 225–237.
- Wikenros, C., Sand, H., Månsson, J., Maartmann, Erling, Eriksen, A., Wabakken, P. and Zimmermann, B. 2020. Impact of a recolonizing, cross-border carnivore population on ungulate harvest in Scandinavia. – *Sci. Rep.* 10: 21670.
- Yrjölä, T. 2002. Forest management guidelines and practices in Finland, Sweden and Norway, vol. 11. – European Forest Institute Sweden and Norway.
- Zimmermann, B., Wikenros, C., Sand, H., Eriksen, A. and Wabakken, P. 2019. Elg i ulvrevir: predaşjon og elgjakt. Utredning om ulv og elg del 2. Swedish University of Agricultural Sciences, Grimsö, Sweden.