Original Research Article

The return of large carnivores: Using hunter observation data to understand the role of predators on ungulate populations

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A R T I C L E   I N F O

A B S T R A C T

Large carnivores play a key ecological role in nature, yet quantifying the effects of predation at large spatiotemporal scales remains challenging. Wolves and brown bears have recovered in Sweden, where they share the same staple prey, moose. This ecosystem is representative of the Eurasian boreal realm, and makes an interesting case study for exploring the use of hunter-collected observation data to understand the ecological effects of large carnivore recovery in human-dominated ecosystems. We used over 50 million hours of moose observation data collected by "citizen scientists" (i.e., moose hunters) between 2000 and 2017 to evaluate the role of recovering bear and wolf populations on an important ungulate vital rate, calf/cow ratio (the number of observed calves per female in fall). Calf/cow ratios were negatively correlated with both wolf and bear densities, suggesting that summer calf survival decreased via predation. Calf/cow ratios decreased by 7% and 17% in the northern and southern areas where bears and wolves were allopatric, respectively. Where wolves and bears were sympatric, the effect of predator densities was additive; calf/cow ratios decreased by 18%. However, both calf/cow ratios and moose densities declined over the last ~20 years across Sweden, including areas where wolves and bears were absent. While recolonizing large carnivores affected ungulate vital rates in Sweden's human-dominated landscape, they were likely not the primary driver of long-term moose population trends. Our results reinforce that citizen-collected data are a useful wildlife monitoring tool that help understand ecological processes, including the effects of recovering carnivores on prey populations.

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1. Introduction

The conservation, recovery, and reintroduction of large carnivore populations have become rallying points for conservationists around the world. Large carnivores fill a key ecological role in nature, and their conservation is considered critical for ecosystem health and function (Terborgh et al., 2001; Wolf and Ripple, 2018). Although many carnivores remain severely threatened (Ripple et al., 2014), the last few decades have seen the partial, ongoing recovery of several large carnivore populations in human-dominated landscapes (Bruskotter and Shelby, 2010; Chapron et al., 2014). Understanding the long-term effect of recovering carnivore populations on prey population dynamics, particularly when located at the human-wildlife interface, is important for the conservation and management of both large carnivores and their prey, as well as for facilitating human-wildlife coexistence (Jonzen et al., 2013; Carter and Linnell, 2016).

However, monitoring broad-scale trends in prey population vital rates is expensive and logistically difficult. Consequently, many studies occur at regional spatial scales or over a limited time period (e.g., Vucetich et al., 2005; Proffitt et al., 2014; Andrén and Liberg, 2015). Long-term and wide-ranging citizen science programs provide a unique opportunity to monitor wildlife populations and trends through time while encouraging stakeholder participation, engagement, and trust (Singh et al., 2014; Cretois et al., 2020). Sweden's unique hunter observation program has worked with hunters since the mid-1980′s to assist monitoring of moose (*Alces alces*) (Ericsson and Wallin, 1999) and brown bear (*Ursus arctos*) populations across the country (Kindberg et al., 2009; Kindberg et al., 2011).

Here, we used this long-term citizen science observation dataset (2000–2017), collected over ~50 million hours by Swedish hunters, to go a step past monitoring and explore how the ongoing recovery of large carnivores affected Sweden's moose population. In our study area, which encompasses Sweden's wolf (*Canis lupus*) recovery area and core brown bear population range (henceforth 'core large carnivore area'; Fig. 1), bear densities and range remained relatively stable over the last 20 years, while wolf densities progressively increased and their distribution expanded to eventually overlap bear range (Ordiz et al., 2015). This inherent spatial and temporal variation allowed us to examine how bear and wolf densities affected an important ungulate vital rate, calf/cow ratio (i.e., the number of observed calves per female moose).

In Sweden, both wolves and bears prey on neonate calves during the moose calving season in late spring and early summer (Sand et al., 2008; Rauset et al., 2012). Calf/cow ratios were recorded during fall and, in the context of large carnivores, reflect the potential effect of neonate predation on summer calf survival. We predicted bear and wolf densities would negatively affect calf/cow ratios both in time and space, and large carnivores would be a key driver of broad-scale calf/cow ratio trends, while accounting for density dependence and weather-related factors. Sweden's ecosystem is characteristic of the anthropogenically influenced Eurasian boreal realm (e.g., where forestry is a major human activity), and our unique, long-term dataset is based on a mutual-trust hunter observation program, which makes this an interesting case study for exploring the use of citizen science data to understand the ecological effects of large carnivore recovery in human-dominated ecosystems.
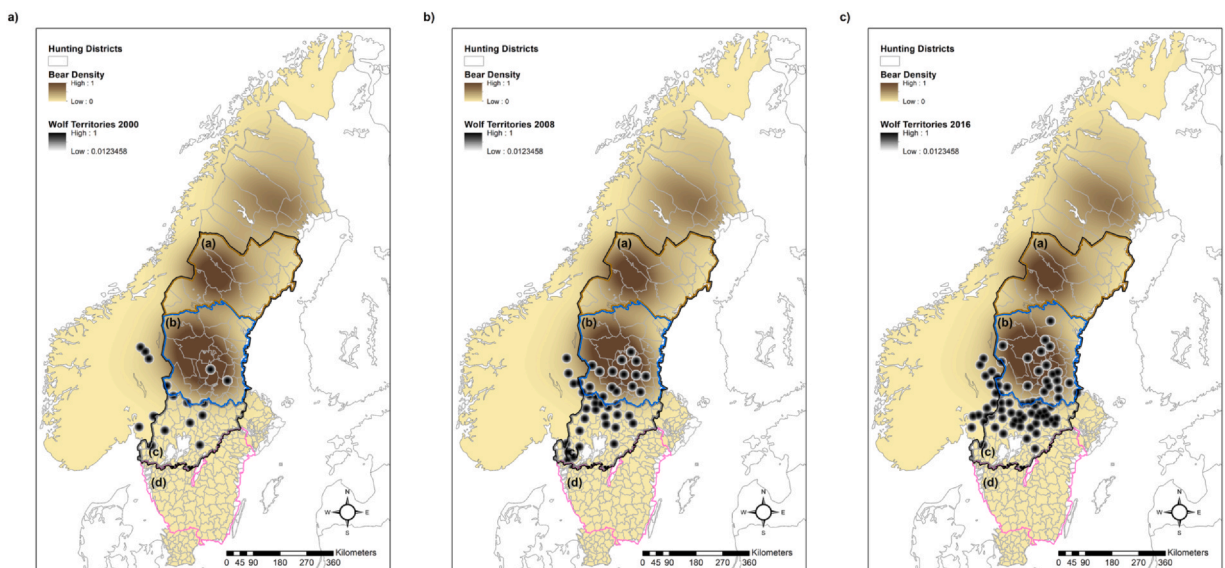

Fig. 1. A time series showing the probability of wolf territory occurrence in Scandinavia towards the a) beginning (2000), b) middle (2008), and c) end (2016) of our study period. All hunting districts in Sweden (light gray) are shown, as well as the core carnivore recovery study area in Sweden (black), the recovery area subsets including the northern (a - brown), central (b - blue), and southern (c - gray) regions, and the region used for comparative purposes outside the recovery area (d - pink). Only hunting districts within the recovery area (black) were used for analysis. For reference, bear densities and wolf territories are displayed across the entire Scandinavian Peninsula (i.e., Sweden and Norway). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Study area

The landscape in Sweden is generally composed of intensively managed boreal forest, primarily Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), interspersed with lakes, bogs, and rivers. The wolf and bear populations in Sweden currently overlap in the northernmost and southernmost extent of their range, respectively (Fig. 1). The wolf population in Sweden was estimated at 44–57 individuals in 1998/1999 and 305 (95% CI= 241–396) in 2017/2018, and their breeding range was limited to south-central Sweden (Wabakken et al., 1999, 2018). Bears are unevenly distributed across the central and northern half of Sweden (Fig. 1), with ~2800 individuals in 2013 and a generally stable population size through time (Kindberg et al., 2011; Swenson et al., 2017). Wolves expanded into bear range near the beginning of the study period, but the number of wolf territories occupying this region remains comparatively low (Fig. 1; Ordiz et al., 2015). We therefore limited our study area to the region in Sweden that either bears permanently inhabited and/or where wolves were recovering over the last 20 years, excluding the northern area in Sweden that extends into the Arctic Circle (Fig. 1). During our study period, licensed hunts were allowed intermittently for wolves (2010, 2011, and 2015–2017; Liberg et al., 2020) and annually for bears (Swenson et al., 2017).

Moose populations in Sweden were low at the start of the 20th century, but quickly started to increase around the 1960′s due to changes in management and forestry practices (Lavsund et al., 2003). Moose reached an all-time high in the early 1980′s after which the population declined, although current moose densities in Sweden are still among the highest in the world (x̄ = 1.3 moose/km^2; Zimmermann et al., 2015). Moose are the main ungulate prey for both bears and wolves in Sweden; both predator species prey heavily on newborn calves during and after the moose parturition period in late spring/early summer, while wolves prey on moose, selecting primarily juveniles, throughout the year (Sand et al., 2005; Swenson et al., 2007; Sand et al., 2008; Rauset et al., 2012).

2.2. Data collection

2.2.1. Observation data

The Swedish authorities and local moose management units use annual hunter observation data, collected by ~200,000 volunteer hunters across the country, to monitor moose and large carnivore populations (Ericsson and Wallin, 1999; Kindberg et al., 2009). Moose observation data were collected by 9460 hunting teams across 292 hunting districts in 20 counties in Sweden during the first 7 active days of the moose hunting season between 2000 and 2017, and reported to the Swedish Association for Hunting and Wildlife Management, who are responsible for these data. The start of the hunting season varied by district, beginning on either the first Monday in September or the second Monday in October. Each day, hunting teams classified and counted the number, age (adult/calf), and sex of moose observed while hunting, and counted the number of brown bear sightings, the number of hunters per hunting team, and their total effort (number of person-hours hunted per day). Harvested moose (shot moose) were classified and counted as 'observed' for the day.

We used the number of observed calves per female (henceforth calf/cow ratio) as a measure of moose calf survival. In Scandinavia, calf/cow ratios are a reliable proxy for moose calf survival, recruitment rate, and population growth (Ericsson and Wallin, 1999; Solberg and Saether, 1999). Hunter observations were conducted after the spring/summer neonate predation period (May-August; Swenson et al., 2007; Sand et al., 2008) and during the first week of that year's moose harvest.

2.2.2. Predator density

An index of wolf territory density was calculated each year between 1999 and 2018 using data collected from annual winter wolf monitoring surveys (Liberg et al., 2012; Wabakken et al., 2018; Wikenros et al., 2020). Here, family groups and scent-marking pairs are located, confirmed, and counted via snow tracking and DNA analysis of scat by technicians employed by the Swedish authorities (for detailed description of monitoring methods, see Liberg et al. (2012)). Locations of packs are registered using Minimum Convex Polygons (MCPs). However, estimating territory size is not the goal of the nationwide monitoring, and MCPs are not reliable proxies for the true wolf territory size, i.e. they are estimated using the outermost located scent-marks of the dominant adults for each territory, and field tracking effort between territories is often uneven. Therefore, following Wikenros et al. (2020), we calculated the probability of wolf territory occurrence in each hunting district by a) buffering the center point of each observed wolf pack by 18 km (the average wolf territory size in Scandinavia, assessed using GPS-telemetry; Mattisson et al., 2013), then b) using a parabola-shaped decay curve to create a decreasing probability of use P_{use} for each territory with increasing distance D from the center point (probability = 1) to the 18 km buffer (probability = 0) (Fig. 1). We used this approximation for wolf territory density because monitoring surveys do not identify complete spatial territory coverage; we assumed the highest probability of territory occurrence was similar to the center of all observations. To approximate annual variation in wolf territory density within each hunting district, we calculated the mean P_{use} for year (t) and (t + 1) inside each hunting district for each year.

Following Ordiz et al. (2015), we used the density of hunter-killed bear locations (1990–2014), which hunters must legally report, to create an index of bear distribution and density (Swenson et al., 1998; Kindberg et al., 2009). Our index ranged from 0 (areas with no or sporadic bear presence) to 1 (areas with the highest bear density). We estimated bear density by calculating the average of this index within each hunting district. We also calculated a bear observation rate (number of bears observed/

hunter effort hours) for each hunting district and year as an alternative proxy for bear density (which reached 30 bears per 1000 km^2) using the observational dataset outlined above (Kindberg et al., 2009).

2.2.3. Moose density

Moose populations are subject to density dependent effects that can alter productivity, recruitment, and population growth (Sand et al., 1996). Hunter harvest statistics are a reliable proxy for relative moose density and overall population trends (Ueno et al., 2014). Swedish hunters are required by law to report the age, sex, and location of all harvested moose to their regional County Administrative Board. Moose harvest statistics for each hunting district in Sweden were downloaded from the County Administrative Board Moose Harvest website (www.algdata.se). We calculated a relative index of moose density for each year by averaging the total number of moose harvested per km^2 of huntable land for each hunting district (Fig. S1) using a one-year time lag (t-1) (see Supplementary Information Section A Moose Harvest Data for further details).

2.2.4. Weather data

Weather data from 1280 weather stations across Sweden were downloaded from the Swedish Meteorological and Hydrological Institute website (www.smhi.se). For each hunting district and year, we calculated the seasonal mean temperatures (°C) during winter (Jan-Feb), spring (Apr-May), and summer (Jun-Aug), the total precipitation (cm) during spring/summer (Apr-Aug), and the average monthly maximum snow depth (cm) during winter (Jan-Mar) from all weather stations located within a 5 km buffer of each hunting district. If a hunting district did not have a weather station located within 5 km, we used measurements from incrementally increasing buffer zones (every 5 km) around the district.

2.3. Data analysis

2.3.1. Temporal trends

To explore trends in calf/cow ratios, and moose, wolf, and bear density through time, we subset our study area (i.e., the primary large carnivore recovery area) into three different regions: a) northern, b) central, and c) southern Sweden (Fig. 1). The latitudinal study area dividers (Fig. 1) represent inherent breakpoints in bear and wolf densities in Sweden; the boundaries between the carnivore recovery areas follow the borders of Swedish hunting districts and were split by maximum and minimum latitudinal boundaries. The a) northern and c) southern areas represent the regions where bears or wolves persisted independently, respectively. The b) central area represents the region where bears persisted, and where wolves expanded into, during our study period. We used the hunter-recorded bear observation data to examine temporal variation in bear density (Kindberg et al., 2009). For comparative purposes, we also report trends from d) outside the recovery area in south and southeastern Sweden, excluding the highly developed Stockholm and Skåne Counties (Fig. 1).

2.3.2. Statistical analysis

We evaluated the effect of bear and wolf density on calf/cow ratios in the core large carnivore recovery area (Fig. 1). To control for imprecision in calf/cow ratios due to insufficient ground observation effort, we limited all analyses to hunting districts/years where total hunter effort was ≥ 5000 h (Ericsson and Wallin, 1999). This resulted in one measurement of cow/calf ratio per district per year, which reflected at least 5000 h of hunter effort, i.e., hundreds of observations collected by multiple hunting teams (Fig. S2). The data were subset to 2004–2017 to test for moose density dependent lag effects up to 5 years.

Our weather metrics included 8 variables that drive moose vital rates in Scandinavia and elsewhere (Grøtan et al., 2009; Monteith et al., 2015). However, all 8 variables were multicollinear and correlated with hunting district latitude. We therefore used principal component analysis (PCA) to reduce the dimensionality of the weather and latitude data while minimizing information loss (Monteith et al., 2015; Jolliffe and Cadima, 2016). The PCA included 9 variables: latitude, the mean spring and summer temperatures (°C) and total summer precipitation (cm) in year (t) and (t-1), and mean winter temperature (°C) and winter/spring maximum snow depth (cm) in year (t) (see Supplementary Information Section B).

Analyses were conducted in R version 3.5.2 (R Core Team, 2018) using generalized linear mixed models (GLMMs) with the 'glmmTMB' package (Brooks et al., 2017). We estimated models with adaptive Gaussian quadrature with parameters estimated from maximum likelihood. Potential variables included bear density (hunter harvest), bear density (observation rate), wolf density, moose density (hunter harvest in years t-1, t-2, t-3, t-4, and t-5), and the first two PCA components (for ranges see Table S2). We used an Akaike information criterion (AIC$_c$) for model selection; the best-fit models had the lowest AIC$_c$ score within a model set, while all models with a ΔAIC$_c$ < 4 were considered plausible (Burnham and Anderson, 2002). All models included an AR1 autocorrelation correction, to control for temporal autocorrelation, and random effect for hunting district ID. We compared models within two univariate model sets to select between bear density proxies (hunter harvest or bear observation rate) and determine the best moose density lag effect; bear density (hunter harvest) and a moose density time lag of t-5 years were included in final model set (Table S3).

Our final model set compared models that represented different combinations of predator (wolf and bear densities) and moose density dependent effects. Because weather varies widely across Sweden's latitudinal gradient, we included PCA components in all predator and density-dependent models. We also included a model that represented weather effects only (PCA component 1–2) and a null intercept only model (see Table S4 for model set). To determine whether the combined effects of wolves and bears on moose calf/cow ratio in our system was compensatory, additive, or supra additive, we also included models with an interaction term for bear and wolf density. If predation was compensatory or supra additive, we would expect to
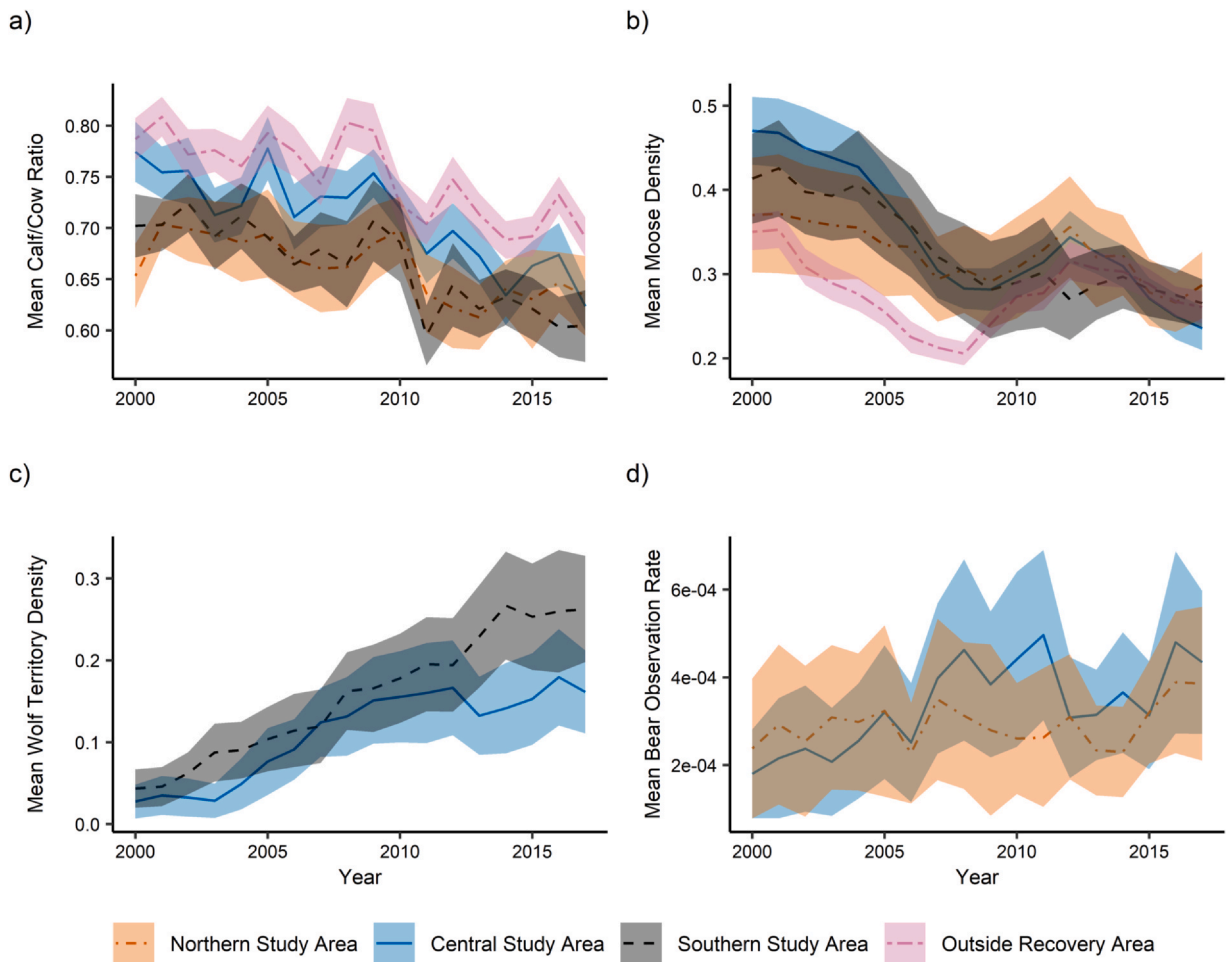
Fig. 2. Temporal trends in mean a) calf/cow ratio, b) moose density (number of moose harvested per km^2), c) wolf territory density (mean probability of territory occurrence), and d) bear observation rate across hunting districts within different regions in Sweden with associated 95% confidence intervals. The northern study area (brown/dotdash) represents where bears are recovering, the central study area (blue/solid) represents the region where both bears and wolves are recovering, the southern study area (gray/dash) where only wolves are recovering, and the area of southern Sweden outside of the wolf/bear recovery area (pink/twodash) for comparison. The portion of southern Sweden outside the recovery area excludes the highly developed Stockholm and Skåne Counties. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

see a significant negative or positive interactive effect of wolf and bear densities on calf/cow ratio, respectively. No evidence of an interactive effect would be indicative of additive predation. We used 95% confidence intervals (CI) to determine the importance of our variables of interest (Fig. 4). All variables were centered and scaled. We also used univariate GLMMs to assess general trends in calf/cow ratios through time in the different regions.

3. Results

3.1. Temporal trends

Calf/cow ratios declined both within and outside the core large carnivore area in Sweden between 2000 and 2017 (Fig. 2a). Mean calf/cow ratios decreased from 0.65 to 0.63 ($\beta = -0.004$; 95% CI= -0.004, -0.003, $p < 0.001$) in the northern area (bears only), from 0.70 to 0.60 ($\beta = -0.007$; 95% CI= -0.008, -0.006, $p < 0.001$) in the central area (bears and wolves), from 0.77 to 0.62 ($\beta = -0.007$; 95% CI= -0.008, -0.006, $p < 0.001$) in the southern area (wolves only), and from 0.79 to 0.69 ($\beta = -0.007$; 95% CI= -0.007, -0.006, $p < 0.001$) outside the large carnivore area in southern Sweden (Fig. S7). Ratios generally (i.e., in most years) remained higher outside the carnivore recovery area than inside (Fig. 2a, S7). Over the same period, moose density (the number of harvested moose per km^2 in year t-1) also declined within and outside the core carnivore area, showing a somewhat similar trend as calf/cow ratios (Fig. 2b). Although calf/cow ratios were higher, mean moose density was lower outside the carnivore area than inside before 2010 (Fig. 2a, b).
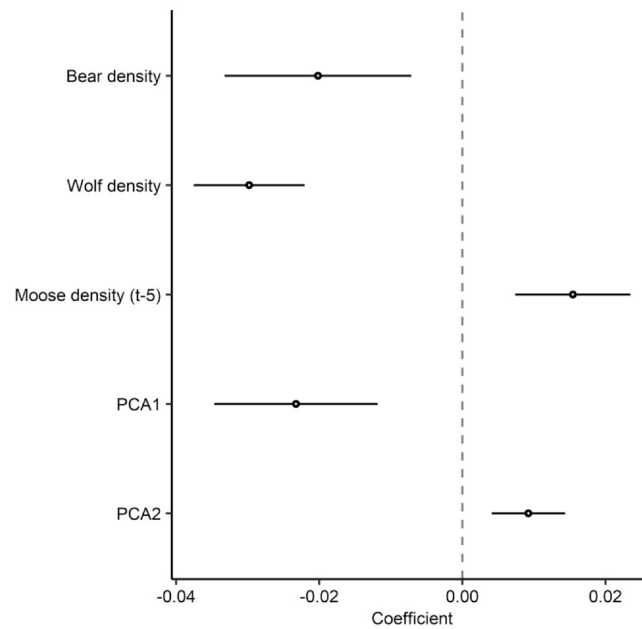
Fig. 3. Parameter estimates with associated 95% confidence intervals for final model predicting moose calf/cow ratios in Sweden. Continuous variables were centered and scaled in all models allowing for comparison of coefficients. PCA 1 and 2 refers to the first two PCA components generated using the weather variables and latitude.

The wolf population in Sweden steadily increased between 2000 and 2015 (Fig. 2c), and then levelled off due to legal harvest and poaching (Liberg et al., 2020). However, wolf density plateaued earlier in the central region where wolves started to expand into bear range (Fig. 2c). Bear densities appeared to remain relatively stable, particularly in the north, with larger oscillations in the central area (Fig. 2d).

3.2. Drivers of calf/cow ratios

The final dataset included 1444 estimates of calf/cow ratios collected in 116 hunting districts within the large carnivore area between 2004 and 2017. Our results suggest large carnivores were an important driver of calf/cow ratios in Sweden. Top models included metrics for both bear and wolf density, outperforming models representing either climate or moose density dependence (Table S4). Calf/cow ratios were negatively correlated with bear density ($\beta = -0.020$; 95% CI= -0.033, -0.007) and wolf density ($\beta = -0.030$; 95% CI= -0.038, -0.022), and the effect of wolves on calf/cow ratio appeared to be greater than that of bears (Fig. 3). None of the top models included an interaction between bear and wolf density (Table S4), suggesting that wolf and bear predation were additive.

With all other variables held at their mean, the highest density of wolves and bears resulted in a 19% (from 0.70 [95% CI 0.69, 0.71] to 0.57 [95% CI 0.54, 0.61]) and 12% (from 0.69 [95% CI 0.68, 0.70] to 0.61 [95% CI 0.56, 0.65]) decrease in the number of calves per cow, respectively, compared to the lowest observed densities. However, observed carnivore densities varied across the carnivore area; a high density of one carnivore did not always coincide with the mean of the other (Fig. 1). In the northern area, with bears only, calf/cow ratios decreased by 7% (from 0.67 [95% CI 0.64, 0.69] to 0.62 [95% CI 0.60, 0.65]) from the highest to lowest observed bear density (Fig. 4a). In the central area, where wolves and bears were sympatric, calf/cow ratios decreased by 18% (from 0.71 [95% CI 0.69, 0.72] to 0.58 [95% CI 0.56, 0.60]) from the highest to lowest observed concurrent wolf and bear densities (Fig. 4b). In the southern area, wolves only, calf/cow ratios decreased by 17% (0.71 [95% CI 0.69, 0.73] to 0.59 [95% CI 0.56, 0.62]) from the highest to lowest observed wolf density (Fig. 4c).

The top model also included a five-year time lag for moose density (Table S3–4), suggesting that the effect of moose density on calf survival and production was delayed. Calf/cow ratios in year (t) were positively affected by moose density in year (t-5) ($\beta = 0.015$; 95% CI= 0.007, 0.024). Weather component 1 ($\beta = -0.023$; 95% CI= -0.035, -0.012) and 2 ($\beta = 0.009$; 95% CI= 0.004, 0.014) were negatively and positively correlated with calf/cow ratio, respectively. Evaluating the strength and directionality of the loadings on component 1 and 2 (Fig. S4–5) suggests that calf/cow ratios generally decreased with increasing latitude, i.e., calf/cow ratios were lower in the north than in the south, which was highly correlated with year-round temperatures; calf/cow ratios increased with increasing temperatures across all seasons. Calf/cow ratios also increased with total summer precipitation in year (t) and (t-1) and decreased with the previous winter's snow depth.
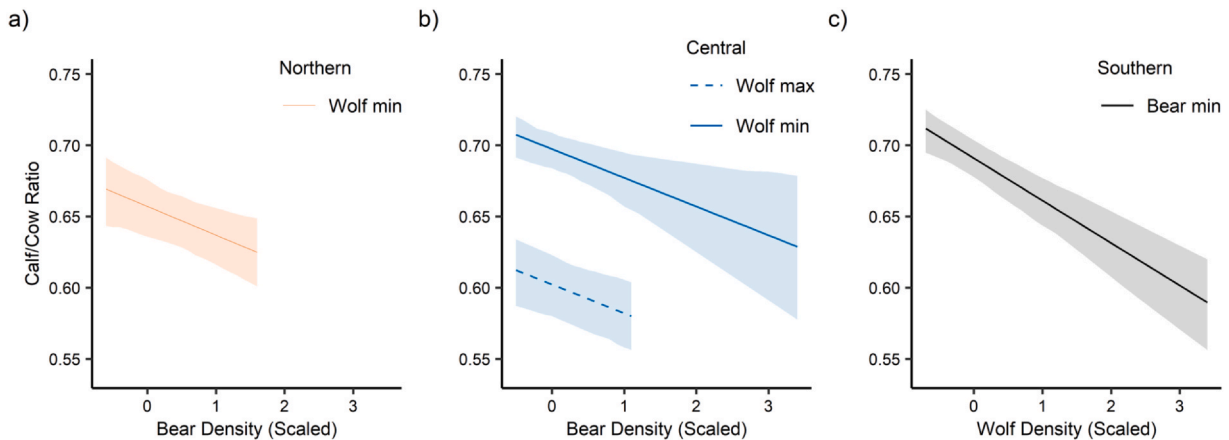
Fig. 4. The effect of wolf and bear density on moose calf/cow ratio in the a) northern, b) central, and c) southern recovery zones where a) bears and c) wolves are functionally allopatric and b) bears and wolves are sympatric. Lines in a) and c) are predicted using population averaged fitted values with associated 95% confidence intervals with wolf and bear density set to the minimum observed value, while lines in b) are predicted using the observed mean of the other values within each region, and the minimum (solid) and maximum (dashed) observed values of wolf densities across the observed range of bear densities in the central region.

4. Discussion

Our results suggest that an important moose population vital rate, calf/cow ratio, was negatively correlated with both wolf and brown bear density in Sweden. Bears and wolves are both efficient predators of neonate ungulate prey (Griffin et al., 2011), including neonate moose in Sweden (Swenson et al., 2007; Sand et al., 2008; Ordiz et al., 2020). Decreased fall calf/cow ratios with increasing wolf and bear densities predominantly reflect the effect of these predators on summer calf survival. For example, in areas where only bears persist in Sweden, bear predation accounted for 61–78% of total summer calf mortality, with the rest attributed to other types of natural mortality (Swenson et al., 2007). Compared to other systems, wolves in Scandinavia focus primarily on newborn moose calves (~90% of wolf kills) during the parturition season (Sand et al., 2008; Tallian et al., 2017). In the absence of predators, moose calf survival is relatively high in Scandinavia, although mortality is greatest during summer (Stubsjoen et al., 2000). While adult female survival is an important driver of ungulate population growth, calf survival often shows greater year-to-year variation, and can explain up to 75% of the variation in population growth rates (Gaillard et al., 2000; Raithel et al., 2007). Thus, wolf and bear predation on neonate moose is likely an important factor affecting moose population dynamics in Sweden.

The effect of wolf and bear density was additive, with the lowest calf/cow ratios estimated for the central area where wolves and bears were sympatric (Fig. 4b). This corresponds to research suggesting that multiple predators can be additive sources of mortality for ungulate populations (Owen-Smith et al., 2005). Elsewhere in Europe, the effect of wolves and lynx (*Lynx lynx*) on roe deer density was greater where both predators were sympatric (Melis et al., 2009). In North America, bear predation on neonate elk (*Cervus elaphus*) was additive to wolf predation, but not vice versa (Griffin et al., 2011). However, competition between predators can have a stabilizing effect on prey population dynamics (Namba et al., 2018). In our system, competition between wolves and bears for shared prey may restrict their cumulative effect on moose population dynamics (Tallian et al., 2017). Furthermore, bears and, especially, wolves are far from reaching carrying capacities in Sweden, where both species are subject to hunting, resulting in restricted range expansion (Ordiz et al., 2015; Swenson et al., 2017). Thus, the potential effect of these species on Sweden's moose population is not fully realized, i.e., their top-down effect would likely be much greater if they were at biological, rather than social, carrying capacity (Ordiz et al., 2013). Interestingly, hunters also appeared to quickly compensate for carnivore recovery by reducing total moose harvest, especially the harvest of prime-aged females, in areas where wolves reestablished (Wikenros et al., 2015), which likely had a compensatory effect on moose population dynamics.

Ungulate population dynamics are driven by a variety of factors other than predation. Our results suggest that calf/cow ratios were density-dependent and increased with a five-year time lag of moose density. A positive density dependent effect was counterintuitive, as moose densities in Sweden are some of the highest in the world (Zimmermann et al., 2015), and the strength of density dependence in ungulates is generally low where large carnivores persist, especially at northern latitudes (Wang et al., 2008). However, negative density dependence generally occurs only at very high moose densities (Saether et al., 1996), and density dependence appears to be positive for many large ungulate populations (Fowler, 1981, 1987). Grøtan et al. (2009) found considerable variation in the magnitude and direction of density dependence on moose recruitment (calf/cow ratio) in neighboring Norway, but their results suggest that positive and negative density dependence were equally likely. They suggest that observed positive density dependence could be the result of a) harvest-driven changes in population age-structure resulting in an increase in prime-age females at high population densities, or b) long lag-times (i.e., > 5 years) between the effect of moose density on forage, coupled with successional changes in forest age composition and forestry practices (Grøtan et al., 2009).

In Sweden, hunter harvest also plays a key role in moose population dynamics, where between about 80,000 and 110,000 moose are harvested each year (Fig. S6). However, it was difficult to tease apart the relative role of moose density and hunter harvest on calf/cow ratios in this study, as the only reliable proxy for moose density across such a broad area was generated using hunter harvest data (Ueno et al., 2014). Thus, the observed effect of moose density on calf/cow ratios should be interpreted with caution, as it is unknown whether it represents time-lagged density dependent food limitation, hunter harvest effects, or both. Furthermore, hunters appeared to quickly compensate for carnivore predation by reducing the harvest of prime-aged females in areas where wolves reestablished (Wikenros et al., 2015), which may also be seen as an indirect carnivore effect; i.e., this compensatory response by humans likely had a stabilizing effect on moose population dynamics in Sweden, but may also have masked the true (larger) effect of predators within our broad-scale analysis.

Weather patterns also influenced calf/cow ratios in Sweden's core carnivore recovery area, likely via multiple pathways. This corroborates research from Norway, where wolves and bears are spatially more restricted and persist at much lower numbers (Bischof et al., 2020), i.e., weather, climate, and density dependence play varied, but important, roles for moose productivity across the latitudinal range of Scandinavia (Grøtan et al., 2009). In our study, mean winter, spring, and summer temperatures (ºC) decreased with the latitudinal gradient and varied between years, but were mostly stable during this period with a few exceptions: winter temperatures dipped in 2010, while summer temperatures peaked in 2002 and 2006 (Fig. S8). Spring and summer total precipitation (cm) and mean maximum snow depth (cm) during winter showed marked variation between years and regions (Fig. S8).

In Sweden, calf/cow ratios increased with total spring/summer precipitation in year (t) and (t-1) (Fig. 3, S4–5). This likely represents the effect of greater forage availability on female body condition during gestation and lactation, resulting in both increased pregnancy rates and calf survival (Testa and Adams, 1998). In addition, and similar to other findings in Scandinavia, previous winter severity, characterized by deep snow-pack and low temperatures, resulted in decreased calf/cow ratio (Grøtan et al., 2009). Severe winters can cause female body condition to decline during mid- to late-gestation, resulting in decreased productivity the following spring (Saether et al., 1996).

Calf/cow ratios decreased with latitude, i.e., from south to north, which likely reflects latitudinal variation in weather patterns and its subsequent effect on forage productivity (Fig. S6). Latitude and winter/spring/summer temperatures were highly correlated and drove the same PCA component, but in opposite directions (Fig. S4). Thus, the overall positive effect of temperature on moose productivity likely represents the broad scale of our analysis and the collinear effect of latitude. Increased moose productivity with high summer temperatures is otherwise a counterintuitive finding, as moose are subject to heat stress and higher parasite loads during warm summers (Monteith et al., 2015; Spong et al., 2020). Indeed, research suggests that high summer temperatures cause moose productivity to decline (Monteith et al., 2015), although this study was conducted at the southern extent of moose range where moose are likely more sensitive to summer heat. However, Grøtan et al. (2009) found the magnitude and direction of the effect of temperature on moose productivity varied by month and across latitudinal gradients in Norway. The effect of temperature most likely varies across Sweden as well, which shares Norway's latitudinal gradient. For example, high summer temperatures in the north may bolster moose body condition via increased forage availability, while high summer temperatures in the south could weaken body condition via heat stress, greater parasite loads, and decreased access to forage.

The use of calf/cow ratios as measures of ungulate survival, recruitment, and productivity has been questioned because calf/cow ratios are inherently unpredictable, as both the numerator and denominator can change independently from one another (Bonenfant et al., 2005). Calf/cow ratios reflect multiple biological processes that are affected by a complex suite of factors, including adult female survival, pregnancy and twinning rates, and calf survival (Harris et al., 2008; Lukacs et al., 2018). Although prenatal factors also influence the calf/cow ratio for moose, calf/cow ratios are generally strongly correlated with calf survival and population growth across an array of ungulate species (Harris et al., 2008), thus are used as a proxy for juvenile survival and population growth in the absence of alternative long-term data (e.g., Proffitt et al., 2014; Monteith et al., 2015; Lukacs et al., 2018). Furthermore, observation data in Sweden have been verified as a reliable tool for monitoring moose population trends (Ericsson and Wallin, 1999).

Moose observations were conducted during fall, which means our knowledge of total calf survival, or recruitment, in Sweden is limited. Fall calf/cow ratios do not account for other sources of calf mortality that occur after the first week of hunting in the fall but before recruitment the following spring, including late fall/winter hunter harvest, which is an important driver of calf survival in this system (Jonzen et al., 2013), and winter mortality, which is less important (Saether et al., 1996; Stubsjoen et al., 2000). Furthermore, unlike bears (Rauset et al., 2012), wolves prey on juvenile moose year-round (Sand et al., 2005, 2008). Together, this implies that spring calf recruitment was much lower than observed calf/cow ratios during the previous fall across the entire study area. This is especially true for areas where wolves recovered, where the observed effect of wolves during the fall hunt is certainly an underestimate of their total annual effect on calf survival.

Although moose calf/cow ratios were negatively correlated with wolf and bear density, both calf/cow ratios and moose densities (i.e., hunter harvest) declined within and outside the core large carnivore area between 2000 and 2017 (Fig. 2a–b). This suggests that moose populations have declined across the majority of Sweden, irrespective of large carnivore recovery and expansion. Potential reasons for the apparent decline of moose densities likely vary across the country, and include a combination of interacting factors. For example, long-lagged negative density dependence, a remnant from when moose persisted at extremely high densities in Sweden during the 1980′s and 1990′s, could potentially effect moose population demography (Lavsund et al., 2003; Grøtan et al., 2009). Shifting forestry practices, resulting in a general reduction of early successional-stage forests and an intentional management shift from pine to spruce, have likely decreased moose forage quality and quantity,

ultimately lowering biological carrying capacity (Lavsund et al., 2003). Increased pressure on managers to mitigate forest property damage (i.e., browse damage) likely resulted in lower societal tolerance and increased hunting quotas. Static sex-specific hunting quotas in a declining population could also alter population structure and lower fecundity (Solberg et al. 2002; Lavsund et al., 2003; Wikenros et al., 2015). This reinforces that while carnivores play a key role in ungulate population dynamics (Ordiz et al., 2021), they can be overridden by anthropogenic effects in human-dominated landscapes (Muhly et al. 2013; Haswell et al., 2017).

4.1. Conclusions

Our study provides novel insight into the effects of recovering large carnivores on ungulate populations by taking advantage of a long-term observational dataset collected by 'citizen scientists' (i.e., hunters). While data collected by citizen scientists are often imperfect (van Strien et al., 2013), such programs are sustainable at large spatial and temporal scales, are low cost, can assist with long-term wildlife monitoring (Cretois et al., 2020; Ražen et al. 2020), and facilitate adaptive management and conflict resolution via active stakeholder engagement (Dickinson et al. 2010; Aceves-Bueno et al., 2015). Our results show that such data can also be used to help understand complex ecological processes, including the effects of recovering carnivores on prey populations at large spatiotemporal scales. Our approach might prove useful in other human-dominated landscapes where some carnivore populations are currently recovering, and where management challenges increase in parallel (Bischof et al., 2020), provided that long-term carnivore and prey monitoring and engagement of important stakeholders is consistently organized.

Declarations

Author contributions

JK, AT, AO, BZ, CW, HS, and PW conceived of the study; AT, BZ, CW, GB, and JK participated in data collection; AT carried out statistical analysis; AT and AO wrote the manuscript; BZ, CW, HS, JK, and PW coordinated long-term research efforts in Scandinavia. All authors helped draft the manuscript and gave final approval for publication.

Declaration of Competing Interest

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01587.

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