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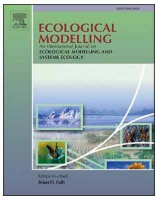

Using citizen data in a population model to estimate population size of moose (*Alces alces*)

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ABSTRACT

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. Hunter observations is such a program that in Sweden is used on a regular basis to monitor population trends of moose. However, hunter observations are not reliable to determine the actual population size. We developed a mechanistic moose population model that integrated citizen science data and used it at various geographical scales to estimate moose population size between 2012 and 2020. A sensitivity analysis, specifically performed for recruitment, adult sex ratio and calf sex ratio, showed that the simulated population size was most sensitive for variation in recruitment. According to the results, Sweden had a total moose population of ~311 000 (± 4%) individuals pre-hunt and ~228 000 (± 4%) post-hunt in 2020. The post-hunt moose abundance has decreased nationwide with 15%, from 0.72 to 0.61 moose per km^2 during the 2012 – 2020 period. The present post-hunt moose density was estimated at 0.39, 0.78, 0.84 and 0.54 per km^2 for the regions northernmost, northern, central and southern Sweden, respectively. The simulation model can be used for strategic and operative management at various geographical scales and is publicly available. By integrating citizen data with a mechanistic population model, a new low-cost method of estimating population size and relevant population dynamics was established.

1. Introduction

Management of wildlife populations needs to be based on reliable monitoring to provide feedback on whether goals are being achieved. Several survey methods are available to estimate wildlife abundance and many of these are based on voluntarily collected data and citizen sciences (Kosmala et al., 2016). Citizen science programs provide a unique opportunity to monitor wildlife populations, explore population dynamics and interactions over large spatiotemporal ranges while also encouraging stakeholder participation, engagement, and trust (Chase et al., 2004; Singh et al., 2014; Cretois et al., 2020,; Tallian et al., 2020).

In Scandinavia, nationwide citizen science programs were launched in the mid-1980′s where hunter observations were collected to support management of moose (*Alces alces*) in Sweden and Norway. Hunter observations of moose are collected during the start of the hunting season in the autumn and provide indices of moose density, post-summer recruitment rate (reproduction minus summer calf mortality), and adult sex ratio (Ericsson and Wallin, 1999; Solberg and Sæther 1999). Both Solberg and Sæther (1999) and Rönnegård et al. (2008) showed that hunter observations can be used to estimate long-term population trends. However, the accuracy of the index is determined by the effort in terms of number of observation hours. It may thereby restrict the use to areas large enough to provide enough observation hours (Ericsson and Wallin, 1999). Differences in observability of animal categories (bulls, cows, cows with calves, etc.) may influence the indices (Solberg and Sæther, 1999). Furthermore, comparing density index between hunting areas is limited by differences in the observability, which in turn is related to hunting methods and type of dominating vegetation (Ericsson and Wallin, 1999). Before comparing density between hunting areas, the index therefore needs to be calibrated with another population estimate. The density index is therefore more suitable for analysis of the temporal trend in population size. However, the determination of ratios between different categories of animals (e.g., sex ratio, females with calves, lone females) is less influenced by differences in observability between areas (Ericsson and Wallin, 1999) and can therefore be used for comparisons across areas.

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Since predictive population models and hunting quotas within management are based on absolute numbers, the indices provided by hunter observations need to be linked to absolute numbers of moose (Månsson et al., 2011). Estimations of moose abundance can be conducted using aerial surveys, pellet group counts or a combination of various sources (Rönnegård et al., 2008) but these methods are associated with different practical caveats and high costs (Månsson et al., 2011). To provide a long-term proxy of the moose population, harvest statistics have been used in Norway and Sweden (Cederlund and Markgren 1987; Østgård, 1987; Lavsund et al., 2003; Ueno et al., 2014).

Population models are an important tool in ecology and wildlife management that can be used to explore dynamics and how management options are related to different factors. Previously, dynamic models on moose have been used to simulate the response of the population given different hunting strategies (Sylvén 1995; Kalén, 2018), changed climate (Rempel, 2011) and different carnivore densities (Crete at al., 1981; Jonzén et al., 2013) but also to evaluate the costs and benefits of aerial surveys in management (Boyce et al., 2012).

The Swedish moose populations began to increase rapidly in the 1960s and have since then been among the most dense, productive, and heavily harvested moose populations in the world (Lavsund et al., 2003) with an estimated number of about 265 000 individuals in 2010 post-harvest (Jensen et al., 2020). Moose management in Sweden is signified by collaborative governance regimes and multi-objective land use (Dressel et al. 2020). Moose provide both ecosystem disservices with economic costs in terms of forest damage and vehicle collisions and services in terms of meat, recreation, hunting and tourism (Gill, 1992; Lavsund et al., 2003; Boman et al., 2011; Bergquist et al., 2019). In Sweden, dense moose populations cause cascading indirect effects on the forest ecosystem (Felton et al., 2019). The return of carnivores such as wolves (*Canis lupus*) and brown bear (*Ursus arctos*) needs increased consideration in management plans as they prey on moose (Rodríguez-Recio et al., 2022).

The Swedish wildlife management system is to a large extent centered around moose. Hunting is the main source of mortality, taking around 25% of the pre-hunt population (Solberg et al., 2000). Since 2012, moose is managed according to an adaptive co-management system to improve the basis for balancing the number of animals to levels that are acceptable with regards to the extent of browsing damage and other societal interests. Moose Management Areas (MMAs, in Swedish Älgförvaltningsområden) represent the focal management unit within the system to initiate management at a larger 'ecosystem scale' (Dressel et al., 2018). Boundaries of MMAs intend to accommodate the migratory behavior of moose by encompassing at least one distinct moose population (Naturvårdsverket, 2011).

In this paper we integrate citizen data (hunter observations) into a mechanistic population model to simulate and estimate moose abundance at various spatial scales in Sweden between 2012 and 2020. Such a model has the potential to produce cost-effective estimates of absolute population size useful for wildlife management. In operational management, a mechanistic model of population dynamics can be useful for examining the effects of alternative hunting quotas and hunting techniques (Kalen, 2018). The incorporation of quantitative data and scientific information into a mechanistic model may reveal gaps in scientific understanding.

2. Methods

2.1. Data

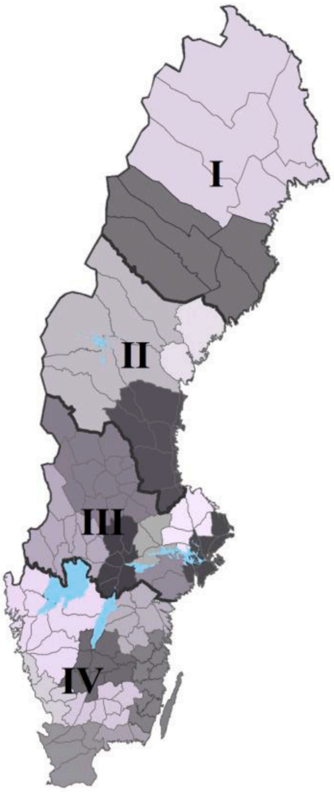

Fig. 1. The management areas (MMA, $n = 131$; gray lines) in Sweden during the hunting season 2020/21. The areas of the MMAs vary between ~250 km^2 and ~30,000 km^2. Gray shading illustrates the 20 counties of Sweden in which the MMAs are managed. The black lines illustrate the four regions: I, Norra Norrland, II, Södra Norrland, III, Svealand and IV, Götaland.

Table 1
Data used for parameterization and validation of the moose population model. Data is available for 131 MMAs in 20 counties. Registered hunting area refers to the total area within each MMA registered for moose hunting.

Category	Variable	Measurement unit	Time specs.
Harvest	Bull	Numbers	2012–2020
	Cow	Numbers	“
	Bull calves	Numbers	“
	Female calves	Numbers	“
Citizen data (Hunters obs.)	Density index	Moose observations per hour hunting effort	“
	Post-summer recruitment rate	Number of calves per cow	“
	Sex ratio adults	Pre-hunt ratio M/F	“
Mortality	Traffic related mortality	Number of bulls, cows, and calves	“
	Wolves	Number of wolf territories	“
	Bears	Number of bears	“
Area	Area of MMA	Hectare	Constant
	Registered hunting area	Hectare	2012–2020

In Sweden, different data is systematically collected for moose management purposes and officially used for local management within Moose Management Areas (MMAs) that also can be linked to counties and regions (Fig. 1). This annually collected data is publicly available and includes harvest statistics, hunter observations, slaughter weight, traffic-related mortality, and registered hunting area (www.älgdata.se) (Table 1). Data is also available on density of large carnivores. We incorporated annual data between 2012 and 2020 into a database which then was used to parameterize and validate a mechanistic population model.

2.1.1. *Hunter observations of moose*

Hunter observations are collected during the first week of the hunting season and are used as one of several tools to find the appropriate harvest quotas in the following year in MMAs. Annually, about five million of observational hours is spent by hunters in Sweden. During this time, about 300 000 observations of moose are registered. Three variables were used as input parameters in the population model: density index, post-summer recruitment rate (calf/cow ratio), and adult sex ratio. Density index is a ratio between the number of observed moose and the number of hours spent by the hunters. Post-summer recruitment rate is measured as the ratio between the number of observed calves and adult females, a measure of recruitment after summer mortality. The number of observed adult males divided by the number of observed adult females constitute the adult sex ratio.

Data was obtained at MMA level and thereafter aggregated to county, region, and national level Fig. 1). In this procedure, data was weighted (ω) by the average of registered hunting area (A) and harvest statistics (H) between the years (y) 2012 and 2020 ($n = 8$ years) (Eq. (1) and ((2)).

$$\omega_i = \frac{\sum A_{i,y}}{n} \times \frac{\sum H_{i,y}}{n} \tag{1}$$

$$X_y = \frac{\sum \omega_i x_{i,y}}{\sum \omega_i} \tag{2}$$

where i is MMA, x is the variable to be weighted and X is the aggregate value. By using weighted data, we found that simulations of population size on the national scale produced consistent results, as when the results were aggregated from either county or regional level. Thus, the simulated population size on the national level was comparable also when summed from the regional or county level. Data of carnivores, harvest, and traffic related mortality was aggregated (summed) to regional and national level without weight.

2.1.2. *Harvest statistics*

Hunters pay an administrative cost to the county council for each harvested moose. Harvest statistics are therefore seen as accurate and include information about the number of harvested adult bulls, females, bull calves and female calves. Although not used in this study, harvest statistics also include information about age, number of antler pins and weight.

2.1.3. *Traffic related mortality*

In Sweden, it is obliged by law to report vehicle collisions with ungulates and large carnivores to the police. A contracted hunter visits the site of collision to track down an injured or dead animal (Seiler et al., 2016). GPS location, time and species involved in the accidents are then reported by the hunter and police to a data base managed by the Swedish National Council for Wildlife Accidents (Nationella Viltolycksrådet; www.viltolycka.se). Data of moose vehicle collisions was obtained for the period 2012 – 2020 for each MMA and was aggregated to county, region, and national level.

2.1.4. *Large carnivores*

In Sweden, brown bears (*Ursus arctos*) prey on moose calves during summer (Rauset et al., 2012) while wolves (*Canis lupus*) prey on juvenile and adult moose year-round (Sand et al., 2005; Sand et al., 2008). For each county we included population data on brown bears (Kindberg et al., 2011; Åsbrink et al., 2021) and wolves (Liberg et al., 2012; Svensson et al., 2021), obtained from official surveys for each county (Wabakken et al., 2020). The population of brown bears is monitored by DNA-based scat surveys in combination with capture-mark-recapture models (Kindberg et al., 2011). An estimate of abundance and trend for brown bears between 2012 and 2020 was compiled for each county by combining population estimates made from DNA analysis with population trends derived from brown bear hunter observations (effort-corrected observations of bears by moose hunters during the moose hunt; Kindberg et al., 2011, and www.viltdata.se).

The total number of wolf territories has been counted each year since 1999 in 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 by authorized county personnel, 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 territories are registered using Minimum Convex Polygons (MCPs) using the outermost located scent-marks of the dominant adults for each territory and was later assigned to different counties based on their geographical location.

Data for the counties Dalarna, Gävleborg, Västernorrland and Jämtland was weighted with area to account for differences in administrative borders and MMA administrative belongings. The compiled dataset is found in Appendix A.

2.2. *Model structure*

The core of the computer model is an age- and sex-explicit structure (i.e., age-classes from 0 to 19 years) modelled separately for males and females and with age-dependent fecundity. Mortality is divided into four categories: hunting, traffic, carnivores, and other mortality. Citizen data on density index, recruitment rate, and adult sex ratio between the years 2012 and 2020 were employed in a fitting technique with parameter modifications to minimize differences between observed and simulated data for these variables. As a result, the simulation model was calibrated to reflect population development and demographic structure between these years. Immigration and emigration were assumed to be equal and therefore not explicitly accounted for. Fig. 2 illustrates the structure of the computer model. The computer model was programmed in Embarcadero Delphi version 10.4 and with a connected MySQL database. The computer model is available for download at www.simthinc.com.

2.2.1. *Recruitment rate*

The total number of new-born calves entering the population is a function of age-specific fecundity (F) and number of cows (n) within each age class (Eq. (3)). The sex-ratio of new-born calves was based on harvest statistics of calves (Moe et al., 2009).

$$Calves = \sum F_{age} n_{age} \tag{3}$$

The age-dependent relationship of fecundity (F_{age}) was based on data from Eriksson and Wallin (2001) and Broman (2002) (Fig. 3), and fitted into a modified double Weibull function (Eq. (4)),

$$F_{age} = a\left(1 - \left(\frac{age}{20}\right)^{b}\right) * e^{-\left(\frac{age}{c}\right)^{-c}} * e^{-\left(\frac{age}{d}\right)^{d}} \tag{4}$$

where b, c and d are constants ($b = 3.4$, $c = 2.5$, $d = 15$). Parameter a was allowed to vary between 0 and 2 during the goal-seeking algorithm (see Figs. 5 and 6). Fecundity is thereby altered uniformly over the age span to obtain the best fit between simulated and observed post-summer recruitment rate.

2.2.2. *Mortality*

Mortality related to carnivores, traffic and other causes is in the model updated twice a year, right before the hunting season (summer mortality) and before calf-birth in spring (winter mortality). The data available on traffic related mortality allows for a division between adults, calves, and sex. The mortality of traffic for each category is distributed equally over the year, i.e., 4/12 during summer and 8/12 during winter.

The number of moose killed by a wolf pack was set to 120 per year (Zimmermann et al., 2014). In summer, 90% is attributed to calves and the remaining 10% to adults without sex or age dependence (Sand et al., 2008). In winter, 80% is attributed to calves and the remaining 20% to adults (Sand et al., 2005).

For bears, the number of killed calves was set to 6 per adult bear and

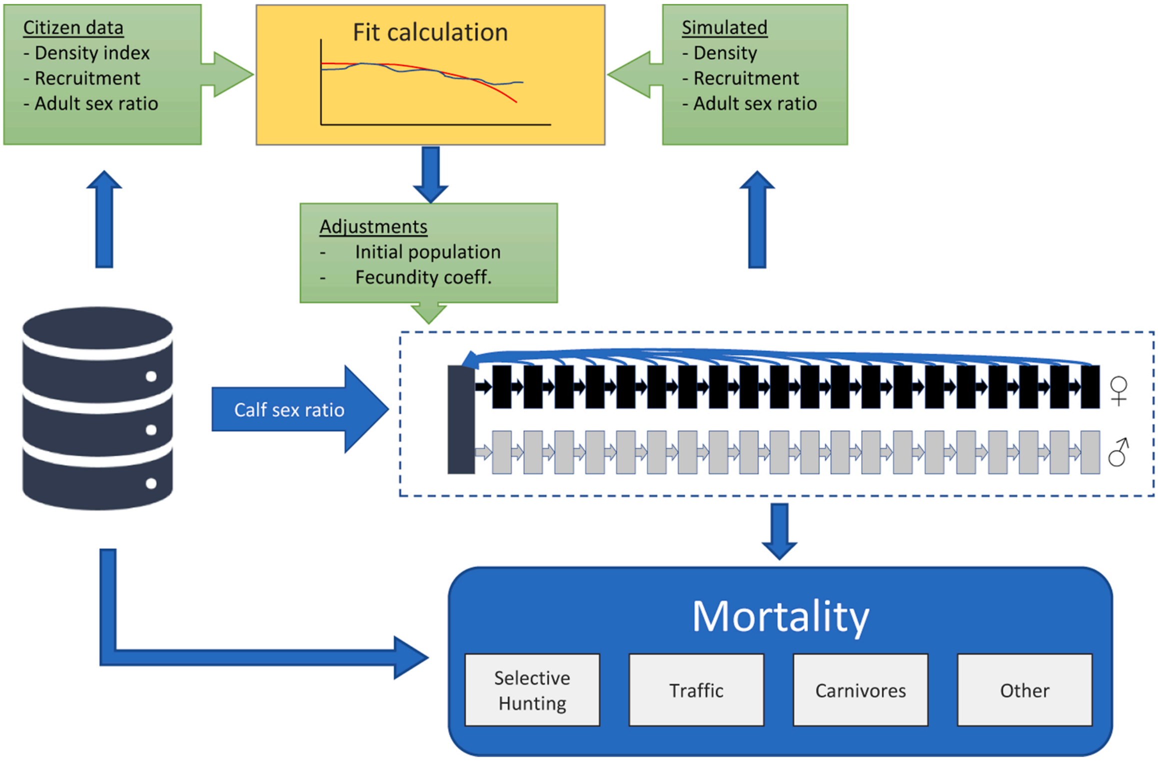

Fig. 2. The moose population is divided into twenty age classes, separated into males and females. Births is calculated from age specific fecundity and number of females in each age class. Annual mortality for traffic, carnivores and other mortality is updated twice a year. Annual harvest statistics is applied once a year to simulate hunting. Citizen data between 2012 and 2020 is compared with simulated density, recruitment rate and adult sex-ratio. An algorithm alters iteratively initial population density and fecundity until the best fit is found.

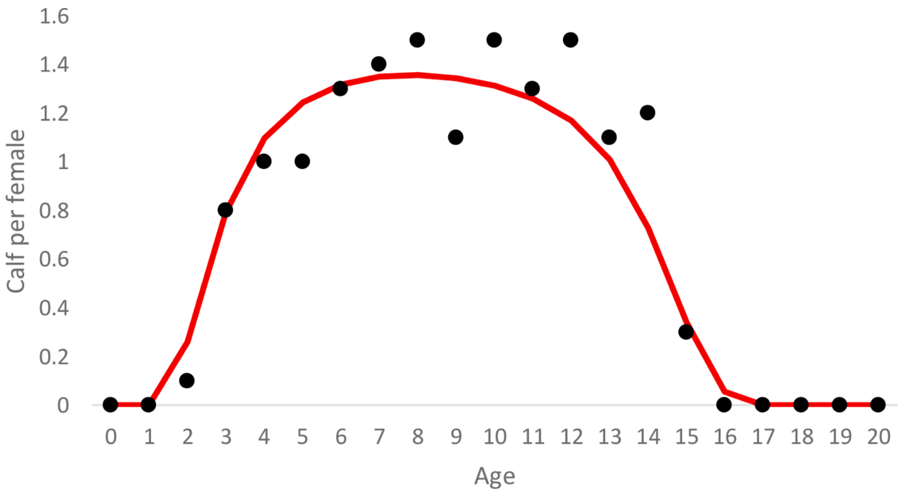

Fig. 3. Fecundity was simulated as age dependent with a modified double Weibull function (red line). Eq. (4) sets the shape of the curve where a is set to 1.5 and is allowed to vary between 0 and 2 during the fitting algorithm. Other parameter values: $b = 3.4$, $c = 2.5$, $d = 15$. Empirical data on fecundity (dots) from Ericsson and Wallin, 2001 for comparison.

year (Rauset et al., 2012). Mortality from bears is only applied to calves during summer.

`Other mortality' refers to mortality not related to hunting, traffic accidents or carnivores. Thus, other mortality is related to starvation, disease, accidents, etc. The official data on other mortality is based only on observed carcasses and therefore incomplete. In previous work where mortality is reported, one must determine if hunting, traffic, or carnivore related mortality is included in the mortality rate. We scrutinized reported mortality rates (Lorentsen et al., 1991; Saether et al., 1996; Stubsjøen et al., 2000; Swenson et al., 2007; Ericsson et al., 2001; Ericsson and Wallin, 2001; Broman et al., 2002; Solberg et al., 2003; Gundersen, 2003; Rönnegård et al., 2008) and from that concluded that other mortality for calves is within the range of 5 to 24% and that adult mortality range between 2 and 7%. Broman et al. (2002) concluded that traffic is responsible for about half of the adult mortality. In the model, calf mortality is simulated with a specific mortality rate (see Table 2), whereas adult mortality rate is simulated as a function of age (Fig. 4).

The age-specific function for mortality rate (m) in adults was slightly modified as compared to Kalén (2018), where a baseline mortality is used in combination with an age-dependent mortality. This modification

Table 2
Mortality rates for causes other than hunting, traffic, and carnivores.

Variable	Carnivores	Base line (%)	Low (%)	High (%)
Calf mortality	Present	5	3	7
Calf mortality	Absent	8	6	10
Adult mortality	Present	3	2	4
Adult mortality	Absent	3	2	4

makes it possible to increase both base mortality and age-dependent mortality with a single parameter, while maintaining the maximum age (Eq. (5)).

$$m = \tau + (1-\tau) * \left(\frac{Age}{Age_{max}}\right)^{(1-\tau)*\left(g-(1000\tau)^{h}\right)} \tag{5}$$

where τ is used to set the mortality rate, Age_{max} (= 19) is a constant that determines the maximum lifespan. To achieve a sensible relationship between base mortality and age-dependent mortality, the constants g and h were set to 16 and 0.55, respectively. Although the maximum age in this way is equal for bulls and females, the proportion of bulls that are older than 15 years during simulations of regulated populations is usually less than 1% whereas this proportion for females usually ranges between 5 and 10%.

2.2.3. Hunting

Annual harvest statistics of bulls, females, bull calves and female calves were applied in the model to simulate hunting in all simulations. A Bayesian approach was used to draw an individual moose from the population where the probability of being selected for harvest is related to sex and age (a more thorough description is given in Kalén, 2018). Except during the initialisation, hunting is thereby specific on individual level and introduces a stochasticity in the model. The model updates the population sequentially after each individual harvest throughout the hunting season, starting in autumn and continues until the harvest quota is reached. The number of individuals remaining after the hunt constitutes the post-hunt population.

In Appendix E (Table E1), assumptions and data sources used for setting mortality is summarised.

2.3. Estimating population size – step one

The population size and recruitment rate in the first year of the simulation period (2012 – 2020) is initially determined by an automated goal-seeking algorithm (Fig. 5). The purpose of this step is to calibrate the population's demographic structure as well as estimate a starting point of population size. This is accomplished by utilizing current data (adult sex-ratio, recruitment rate, mortality, harvest, etc.). This algorithm relies on the assumption that a population can be maintained at a steady state with a specific annual harvest. The population size is set by a sub-algorithm iteratively seeking a specific annual harvest that fulfills the target steady state population (see Appendix D). Data on adult sex ratio, calf sex ratio and other mortality is used for parameterisation and held as constants throughout this step. Net recruitment rate is calculated when the population reach a steady state. The goal seeking algorithm adjusts the steady-state population size and reproduction coefficient (a in Eq. (4)) iteratively to find a predetermined value of harvest and net recruitment rate. Estimating abundance in step one ends when harvest and recruitment rate is equal to values specified a priori (i.e., actual data derived from harvest statistics and hunter observations).

For example, in Uppsala County, the harvest and recruitment rate were reported to be 0.21 moose per km^2 and 0.72 calves per adult female in 2012, respectively. As shown in Fig. 5, the algorithm starts with finding a population density at a steady state that meets the reported harvest of 0.21 moose per km^2. When this is found the model continues to adjust the recruitment rate coefficient until the reported value of recruitment rate (0.72) is found, also at a steady state. However, as soon as recruitment rate is altered, it will affect the annual harvest needed to maintain the target population. The model therefore seeks a new value of the population density that corresponds to the reported harvest. When both annual harvest and recruitment rate equal the reported values, the algorithm ends, and the values of the population size and recruitment rate coefficient are used in step two.

2.4. Estimating population size – step two

The purpose of step one is to achieve an estimate of population size and demographic structure only to be used as start values in the second step, where a fitting algorithm is performed with support of a time series of actual harvest statistics. An aggregated time series between 2012 and 2020 for the variables specified in Table 1 was used to parameterise the model for the twenty counties, four regions, and at national level. For each area, the simulated density and recruitment rate was validated by optimizing the fit of population index (i.e. moose observations per hour), post-summer recruitment rate and adult sex ratio, also included within the time series. The trend of simulated density and recruitment rate will be matched with actual data by iteratively modifying parameters setting initial density and recruitment rate prior to applying

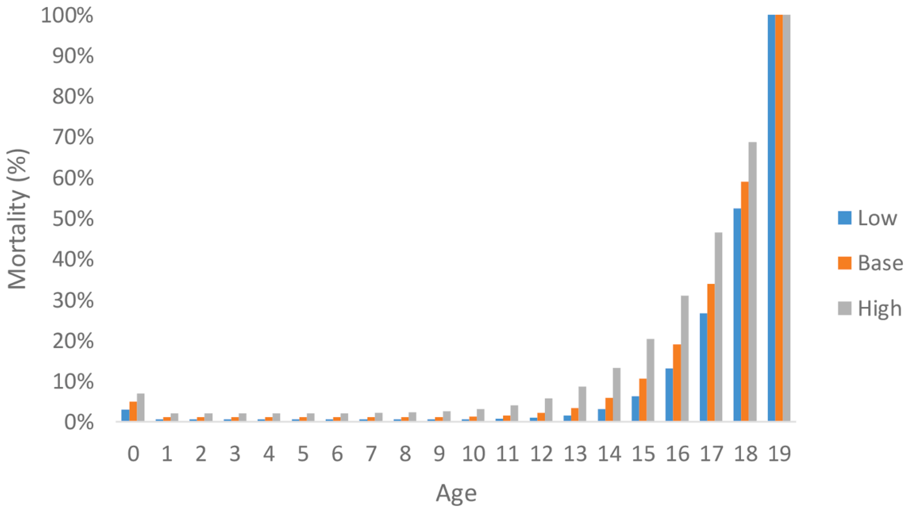

Fig. 4. Other mortality (starvation, disease, age, etc.), not related to hunting, traffic accidents or carnivores, is simulated with a function of age. Calf mortality (age=0) is specified separately from the function used for adults. Three different mortality rates (low, base, high) were used during simulations (Table 2). .

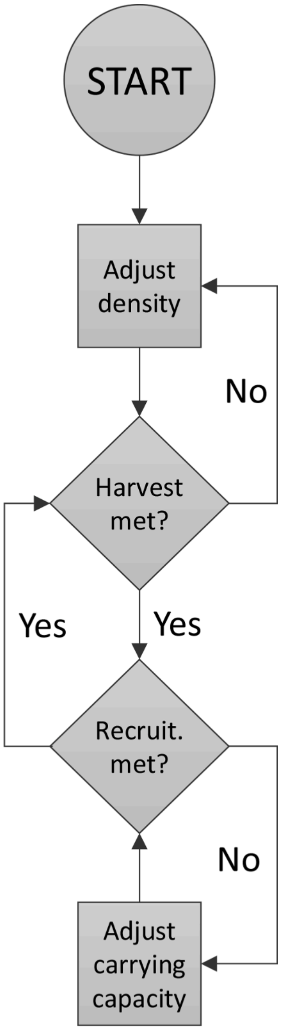

Fig. 5. The goal-seeking algorithm aimed at fitting the harvest and recruitment rate reproduction with data obtained from harvest statistics and hunter observations. In this algorithm, the model sets a steady-state density and finds a stable harvest level to achieve the desired density.

harvest and mortality data between 2012 and 2020 (Fig. 6). The fit of each factor (*j*); population development, recruitment rate, and sex ratio were evaluated with Eq. (6).

$$R_j^2 = min\left(1, \frac{\sum (x_i - y_i)^2}{\sum (x_i - \bar{x})^2}\right)^2 \tag{6}$$

where x_i is the simulated value in year *i*, y_i the observed in year *i*. The three R^2 values were individually weighted before being integrated into an overall model fit (i.e., density (weight=6) and recruitment (weight=4) were prioritised over sex ratio (weight=1)). Solberg and Sæther (1999) concluded that there was an 85% chance that a positive or negative change in population density was followed by an equal change in density index. We therefore attributed this factor to the highest weight. Differences in recruitment rate have higher relative impact on population dynamics than the sex-ratio, which motivates a higher weight attributed to this factor compared to the adult sex-ratio. As each factor may vary independently during the fitting process, an integrated R^2-value was applied to optimize the overall fit of the three factors. The algorithm ends when the integrated R^2-fit does not improve within thirty iterations. It is worth noting that the simulated trend of adult sex-ratio is not influenced by any parameter, but rather is the consequence of sex-specific adult harvesting during the simulation period.

Prior to calculating the fit, the observed density index (*D*) was transformed to the same scale as simulated pre-hunt density (*d*) (Eq. (7)).

$$y_i = D_i \times \frac{\sum d_i}{\sum D_i} \tag{7}$$

where y_i is the transformed value of observed density index in year *i*. This transformation will produce an identical mean for *y* and *d*.

2.5. *Mortality scenarios*

To account for uncertainty in other mortality, we ran simulations with three different levels of other mortality (Table 2). We used a lower mortality rate for calves in areas where carnivores are present to account for compensatory mortality.

2.6. *Validation and sensitivity analysis*

The model was validated with independent population census in Jönköping County estimated by group pellet count (see Appendix B) prior to running the model with data for all counties, regions and at the national level.

A sensitivity analysis of citizen data was performed at national level on recruitment rate, adult sex ratio (obtained from hunter observations) and calf sex ratio (obtained from harvest statistics). Population estimates were obtained after parameter values were decreased or increased separately by 10% prior to each run. The average parameter data between 2012 and 2020 on the national scale for recruitment rate (calf per cow) was 0.62, adult sex ratio[1] (M/F) 0.57 and calf sex ratio (M/F) 1.06. For comparison, the national targets for recruitment rate and adult sex-ratio are set at >0.6 and >0.54, respectively (Naturvårdsverket 2018).

3. Results

Mean hunter observation, aggregated for all Sweden, decreased from 0.053 observations per hour hunting effort in 2012 to 0.046 in 2020. This corresponds to a 13% overall decrease or a 1.8% annual decrease. The simulated post-hunt moose population in Sweden decreased from ~270 000 to ~228 000 individuals between 2012 and 2020, which corresponds to a 15% decrease or a 2% annual decrease. The 2020 pre-hunt density was estimated to 0.83 per km^2, which is a 14% drop from 0.97 per km^2 in 2012 (registered hunting area was in 2020 approximately 375 000 km^2). The post-hunt population density decreased from 0.72 per km^2 in 2012 to 0.61 per km^2 in 2020. The simulation model was able to iteratively converge to a good fit between pre-hunt density ($R^2 = 0.973$), recruitment rate ($R^2 = 0.989$), adult sex ratio ($R^2 = 0.996$), and their counterparts as derived from the hunter observations (Fig. 7).

Running the model with high and low levels of other mortality resulted in a deviation of about ±4% of the final population estimate as compared to the base scenario (see Table 2).

The sensitivity analysis showed that simulated population size was about twice as sensitive to deviations in recruitment rate as compared to the adult sex ratio. Calf sex ratio, obtained from harvest statistics, showed the lowest sensitivity of the tested parameters (Fig. 8).

In accordance with the population trend at the national level, the simulated population development for the four sub-regions also showed

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[1] In Sweden, the proportion of bulls in the adult population is used rather than the male-female ratio (r). To convert to proportion (p) use p=r/(1+r).

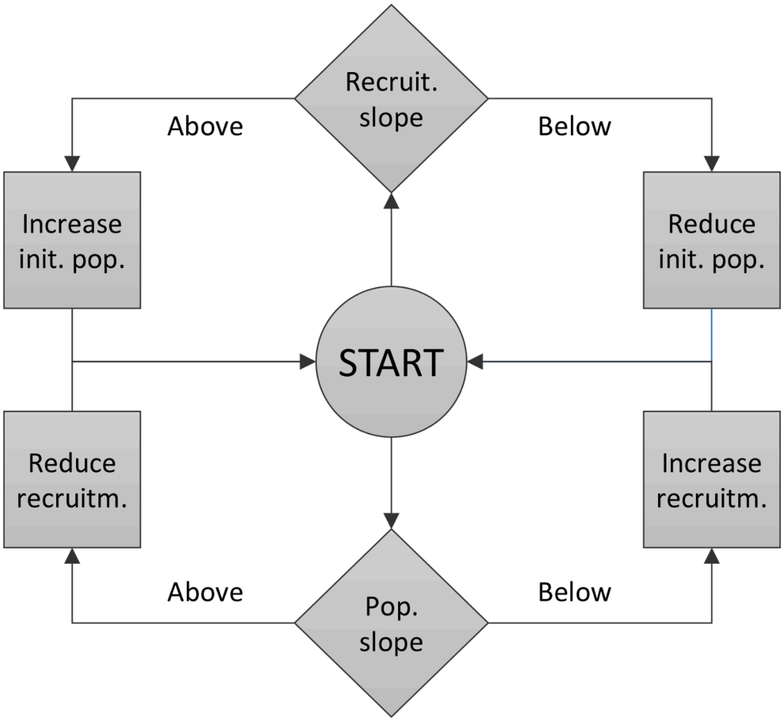

Fig. 6. The goal seeking algorithm in the second step seek to find the best parameter fit for the population development and recruitment rate trend.

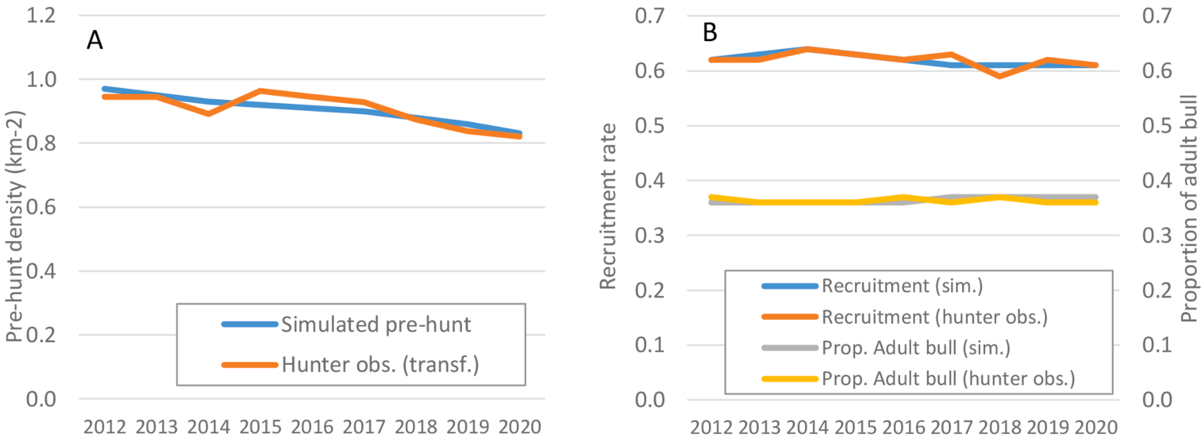

Fig. 7. The simulated and observed trends of (A) pre-hunt moose population density and (B) recruitment rate (number of calves per female) and the proportion of adult bulls at a national level during 2012 to 2020 in Sweden.

a decreasing trend. The result obtained when simulated at a regional level was consistent with simulations at county level and later summed to the regional level (Fig. 9). The estimated population in 2020 for each sub-region simulated with different values of mortality other than related to hunting, carnivores and traffic is presented in Table 3. In Appendix C, simulation estimates for the twenty counties are listed.

4. Discussion

In this study we demonstrate how to estimate the population size of moose at various geographical scales by combining citizen science data, in terms of hunter observations, with other sources of data in a mechanistic population model. The model converged to a good fit in all variables used for parameterisation and validation (i.e. moose density index, recruitment rate and adult sex ratio). According to model estimates, the moose population in Sweden was ~311 000 (± 4%) individuals pre-hunt and ~228 000 (± 4%) post-hunt in 2020, and that the population has decreased with 15%, or 2% per annum, since 2012. The total number of harvested individuals in 2020 was 82 827, which means that 27% of the summer population was harvested. The population estimate is in line with earlier estimates (Jensen et al., 2020). Each of the four regions showed a decrease but with different magnitudes (21, 16, 7 and 20% for northernmost, northern, central, and southern Sweden, respectively). The objective in most MMA during this period has been to lower the moose population to alleviate browsing damage on young Scots pines (*Pinus sylvestris*). Consequences of browsing damage on pine

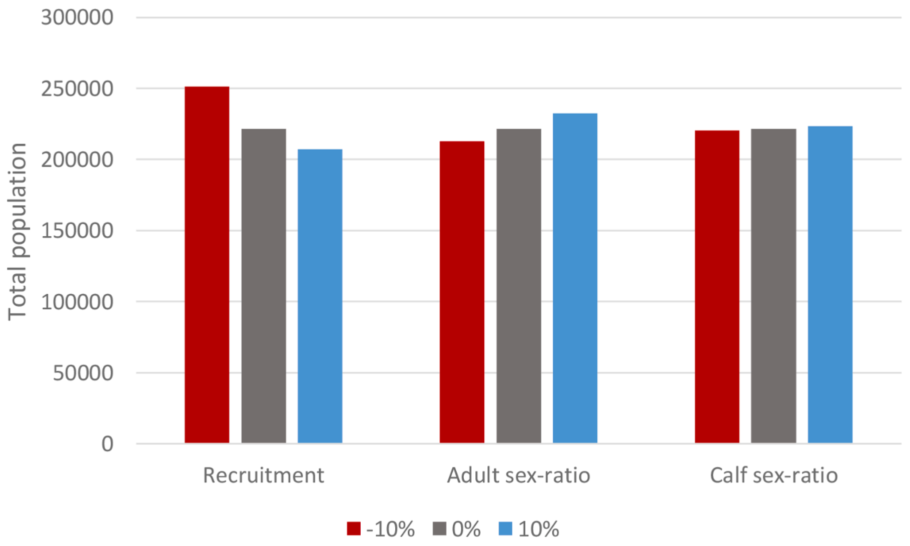

Fig. 8. Results of the sensitivity analysis of total moose abundance in the year 2020 in relation to accuracy of the three input parameters: recruitment rate, adult sex ratio and calf sex ratio. A 10 percent deviation (blue=positive and red=negative) in these parameters affected the estimated total population. Note that a lower recruitment rate will result in a higher population estimate, as more animals are needed to sustain the total mortality from hunting, carnivores, and traffic.

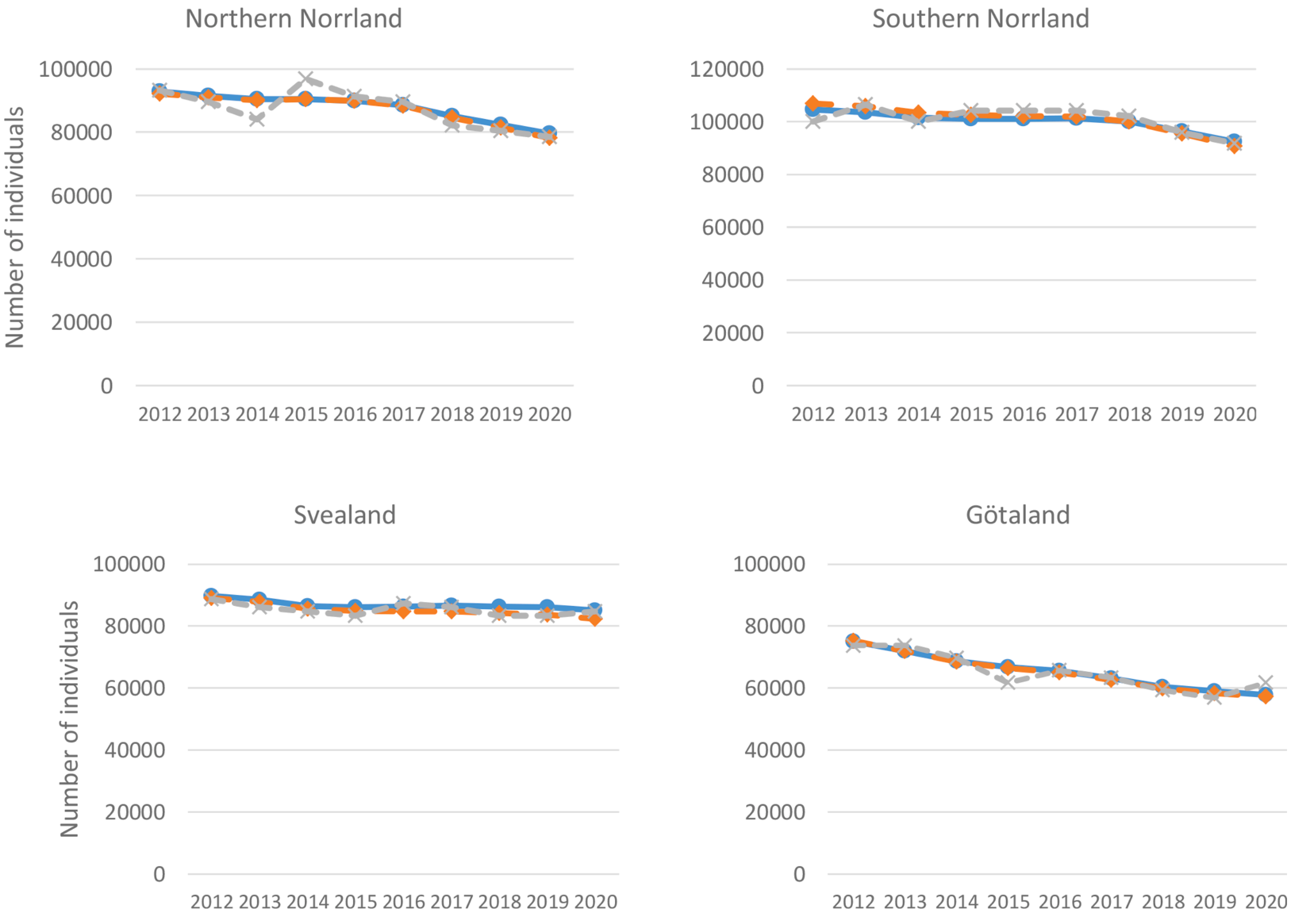

Fig. 9. Simulated trends of the number of moose pre-hunt in four different regions in Sweden during 2012–2020. Dashed line (◆) represents simulation at regional level and solid line (●) represents the sum of simulations on the county level within the specific region. For comparison, a transformed dashed line of hunter observation is included (×).

Table 3
Simulated result of present pre-hunt and post-hunt number of moose in the four main regions in Sweden. Low, middle, and high denotes different assumptions of the level of other mortality. Reg. Area is the total area registered for moose hunting.

	Pre-hunt			Post-hunt			Reg. Area
Region	Low	Middle	High	Low	Middle	High	(km^2)
Norra Norrland	76 586	79 319	82 787	50 766	53 499	56 967	132 893
Södra Norrland	90 775	92 654	93 074	67 181	69 059	69 479	86 350
Svealand	80 686	83 295	87 682	62 573	64 995	69 569	76 640
Götaland	55 770	57 178	59 078	40 479	41 904	43 753	78 261
Total	303 817	312 446	322 620	220 999	229 456	239 767	374 144

are related to high economic losses for the forest industry (Bergquist et al., 2018). A recent report concluded that the moose population decreased by 10% between 2014 and 2020 (Widemo et al., 2022).

The sensitivity analysis revealed that the model estimate was most sensitive for variation in recruitment rate (calves per female) followed by adult sex-ratio and calf sex-ratio. Inaccurate parameter data will therefore influence the population estimate but to various degrees. For example, if recruitment rate is underestimated, the abundance will be overestimated and vice versa. Reproduction in moose have shown considerable variation among local populations and over time due to density dependent processes or climatic variation within Scandinavia (Sand and Cederlund, 1996; Sand et al., 1997; Solberg et al., 2006; Grøtan et al., 2009). Significant variation in moose population productivity has also been documented in North America (Ferguson, 2002).

Likewise, if the proportion of males is overestimated, the simulated population size will also be overestimated. The observational data on the sex-ratio may be biased due to behavioural differences between adult males and females. This can be particularly apparent in relation to when the first hunting week occurs in relation to the rut during which males are known to be more active than females (Cederlund and Sand, 1994). Solberg et al. (2010) found a consistent over-estimation of the proportion of males in the hunter observations. However, based on the consistency between the simulated and observed sex-ratio, we did not find any indication of a systematic or consistent bias in the adult sex-ratio. The population estimate was least sensitive to calf sex-ratio. The low sensitivity in this variable indicates that it is possible to use a constant if annual estimation of calf sex-ratio is missing. Based on harvest statistics at a national level, the average sex-ratio for calves (M/F) was 1.06 between 2012 and 2020 (i.e. 51.5% male calves).

We used hunter observations to both parameterise and validate the model. Validation with independent data at a national or regional scale is not possible as other sources of population estimates are unavailable. The aim of our population model was to simulate net recruitment and mortality with relevant mechanistic causal relationships and with available parameter data to come as close as possible to the true net population growth. Validating not only with density index (moose observations per hour hunting effort), but also recruitment rate and adult sex ratio narrows down the plausible outcomes of the model as these will affect both growth and abundance. Prior to running the model on a national and regional scale, we validated the model with data from Jönköping County where high consistency in both estimated population size and trends were obtained (Appendix B).

In addition to being non-randomly sampled in space and time, the use of hunter observations in local management is limited by the uncertainty derived from low hunting effort (the total number hours of observation). While Moose Hunting Areas (a subdivision of MMAs) usually are the smallest operational unit where harvest quotas are set, the recommended number of observational hours per year (5000) is often not achieved to produce reliable trends (Ericsson and Kindberg, 2011). Therefore, there is a limitation to when and where the model described here is applicable. Already at the MMA level, there are areas where observation data fluctuates more between years than what should be expected from actual changes in moose abundance. This will introduce additional uncertainty into the model results.

According to findings during our analysis, we suggest that hunter observations should be weighted with area and harvest statistics when aggregated to a higher level, i.e., from MMA, to county and so forth. When observations were weighted before being aggregated to a higher level, the simulated results of the total moose population were essentially the same when summed to the national level from either county or regional level. The theoretical argument for weighting hunter observations is that the number of moose observations is determined by the number of moose and the number of hunters contributing to the statistics. Area, although correlated, does not in itself contribute to moose observations and therefore needs to be accounted for when aggregating two areas of different size. Furthermore, a productive area in terms of annual average moose harvest should have a higher influence on moose density index (number of moose observed per hour) when aggregated with a less productive area of equal size. The reason being that the former is likely to have a denser moose population than the latter.

In our study, a constant was used to set the number of moose killed by large carnivores during the simulations. However, wolf and bear impact on the local moose population in Scandinavia may range from low to high depending on their density and the presence of alternative prey species (Wikenros et al., 2015, 2020; Tallian et al., 2021). Indeed, wolves and brown bears have shown to have a major limiting effect on moose populations in North America sometimes preventing further growth in the moose population (Boertje et al., 2009, 2010). In areas in Scandinavia where the presence of other deer species is substantial, the number of killed moose per wolf territory is likely to be reduced due to the observed ability for wolves to switch prey from moose to smaller deer where they are sufficiently abundant (Sand et al., 2016). At present, wolves are mainly concentrated in moose dominated areas, but as the wolf population expands to the south, other deer species become more abundant. Therefore, we would need to include more detailed data on the rate and composition of prey species killed by wolves in this part of the country (Rodríguez-Recio et al., 2022).

As the estimate of population size is derived while applying actual harvest statistics, our model may also be used in moose management to set harvest quotas to achieve a specified population density and sex composition. An important objective in Swedish moose management is to balance moose density with forest damage. One way to alleviate browsing damage is by reducing the moose population, regardless of its actual size. It is in this perspective more relevant to manage the population trend than absolute numbers. A specific feature of our model is that the simulated population trend is robust to changes in parameter assumptions such as for mortality. That is, although running the model with a different mortality, the fitting algorithm will result in the same population trend (not size). This may be counterintuitive at first, as the same harvest is applied during simulation. However, it is explained by the fact that both population density and recruitment rate are adjusted during the fitting algorithm and therefore able to adapt to various levels of mortality. From a management perspective, this is of benefit when analysing the effect of different harvest quotas on population development.

Population trajectories based on hunter observations have uncertainties. Analysis of long-term ecological studies have shown that trends that are identified in a short period ("broken window") can be misleading (Bahlai et al., 2021). The optimal time span to be used with hunter observational data to detect a consistent trend has not been tested. It will to some extent be dependent on the number of observational hours used to obtain the data. In our analysis we aggregated data to county level as the smallest unit. The average number of observational hours spent annually between 2012 and 2020 at county level was ~240,000, which is far above the recommendation of at least 5000 h. On this level, we propose that simulations should be done with a minimum of four years of data. However, to avoid too much influence from systematic bias and annual stochasticity (e.g. erroneous data, influence of weather, immigration and emigration) there is also an optimal upper limit for using trend data in our simulation model. We propose that the best interval for trend data in our simulation model is between 5 and 8 years. This would also be applicable to MMAs.

A fundamental goal in population ecology is to understand how populations are regulated (Newton, 1998). Development of methods to improve the precision of population estimates has become increasingly important in wildlife management in collaborative governance regimes and multi-objective land use (Dressel et al., 2020, SEPA 2018). Citizen science data can contribute with cost-effective data for use in operative management (Szabo et al., 2013). Previously, citizen data has been used in non-mechanistic integrated population models to estimate population development (Rönnegård et al., 2008). Using a mechanistic and dynamic systems approach, where causal relationships are explicitly simulated, has the benefit of being more straight forward as compared to the complexity of incorporating feedback mechanisms in matrix algebra (Davis and Kessler 2016). In addition, as several demographic entities are integrated into our model (demographic structure, average age, adult sex-ratio, recruitment rate), it allows for the possibility to explore various demographic processes within a population (Schaub and Abadi, 2011). A possible further development of the model is to integrate landscape features for exploring forest damage, carrying capacity dynamics, and alternative causes of actions in moose management. Apart from fostering understanding of such processes, such a model has the potential to be a valuable tool in operative management to map population trends, analyze harvest strategies and to set new management goals.

5. Conclusion

Citizen data has the potential to support management and conservation by covering vast spatial and temporal scales not economically feasible to cover by other means. In our study we show one way of integrating citizen data in terms of hunter observation into a population model to estimate moose abundance at various scales. As the simulation was performed by applying actual harvest statistics, the model can also be used to forecast population development at a given sex- and age-differentiated harvest and recruitment rate.

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CRediT authorship contribution statement

Christer Kalén: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing. **Henrik Andrén:** Methodology, Formal analysis, Supervision, Writing – review & editing. **Johan Månsson:** Methodology, Writing – review & editing. **Håkan Sand:** Methodology, Resources, Supervision, Writing – review & editing.

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Data Availability

Data is publically avalibable. Links are included.

Appendix A. Estimated population development of bears and wolf territories

Table A.1 and Table A.2

Table A.1
Estimated development of bears in counties where bears are present. The estimated population reported from surveys are written in bold letters.

Year	Norrbotten	Västerbotten	Jämtland	Västernorrland	Gävleborg	Dalarna	Värmland
2012	534	434	1005	182	268	302	2
2013	527	447	1026	188	324	308	3
2014	520	461	1047	194	380	314	5
2015	513	474	1069	200	435	320	7
2016	**506**	488	1090	206	491	326	9
2017	499	501	1111	212	547	332	**11**
2018	492	515	1132	218	602	338	13
2019	485	**528**	1153	225	658	343	15
2020	478	541	1175	231	714	349	17

Table A.2
Estimated development of wolf territories in counties where wolves are present.

Region	County	2012	2013	2014	2015	2016	2017	2018	2019	2020
Norra Norrland	Norrbotten	0.5	0	0	0	0	0	0	0	0
Norra Norrland	Västerbotten	0.5	0	0	0	0	0	0	0	0
Södra Norrland	Gävleborg	3	4.5	6	8.5	7	7	8.5	12.5	9.5
Södra Norrland	Jämtland	3.5	2	0.5	2.5	3	1	2	2	1.5
Södra Norrland	Västernorrland	0.5	1.5	0.5	1	0.5	0	0.5	0.5	0.5
Svealand	Dalarna	13.5	15	14	17	16.5	10	7	10.5	10.5
Svealand	Stockholm	1	0	1	0	0.5	0.5	0.5	0.5	0.5
Svealand	Södermanland	0	0	0	0	0.5	2.5	1.5	1.5	1.5
Svealand	Uppsala	0	0	0.5	0.5	0.5	0.5	0.5	1	1
Svealand	Värmland	20	22	20	21	19.5	22	20.5	17	17.5
Svealand	Västmanland	3	3.5	5	4.5	4.5	6	4.5	4	4.5
Svealand	Örebro	7	9	8.5	5.5	7.5	7	6.5	8	9
Götaland	Blekinge	0	0	0	0	0	0	0	0	0
Götaland	Halland	0	0	0	0	0	0	0	0	0
Götaland	Jönköping	0	0	0	0	0	0	0	0	0.5
Götaland	Kalmar	0	0	0	0	0	0	0	0	0
Götaland	Kronoberg	0	0	0	0	0	0	0	0	0
Götaland	Skåne	0	0	0	0	0	0	0	0	1
Götaland	Västra Götaland	2	3	2	0	1.5	1.5	1	1.5	2.5
Götaland	Östergötland	0	0	0	0	0	1	1	1	1
Total		54.5	60.5	58	60.5	61.5	59	54	60	61

Appendix B. Model validation via pellet count

The pellet group count method is an established method to estimate moose density and is commonly used in within the Fennoscandian moose management (Neff 1968, Wennberg DiGasper 2006, Rönnegård et al., 2008). In Jönköping county, a pellet group count is voluntarily carried out by hunters on an annual basis. The county administration receives the data and produces an annual report. The sampling method is based on permanent 1 × 1 km squares systematically distributed over the area (i.e. a moose management unit or a moose license area). Each square has 20 (five along each side) permanent circular sample plots of 100 m^2. In 2020, data on 75 565 plots were sampled within the county. To register a single pellet group count, a minimum of 20 pellets should be identified. The density (D) measured as moose individuals per km^2 is calculated with Eq. (B.1),

$$D = \frac{10000p}{dPf} \tag{B.1}$$

where p is the total number of moose pellet groups found, d is days since the plot was cleared from pellets in the autumn, P is the total number of plots and f is a constant representing the number of droppings per moose and day. The constant f (defecation rate) has a large influence on the final density and studies have found it to vary between 14 and 23.5 (Härkönen and Heikkilä 1999; Matala and Uotila 2013). In Jönköping's county, two alternative values of defecation rate are officially used to estimate the density of moose; 17 and 19. In diagram B.1 results from the moose pellet count is given with these two values of the constant together with result from estimating the density through the model described in the paper.

The simulated moose density corresponds well with the moose pellet group count census (Fig. B.1). The simulated post-hunt population was closer to the trend derived from pellet count. However, the negative slope of pre-hunt simulation is more aligned to the slope of the trend of pellet counts. One explanation for this is that the pellet count is not solely an estimate of post-hunt density. Instead, the trend derived from moose pellets may be a mixture between pre- and post-hunt density.

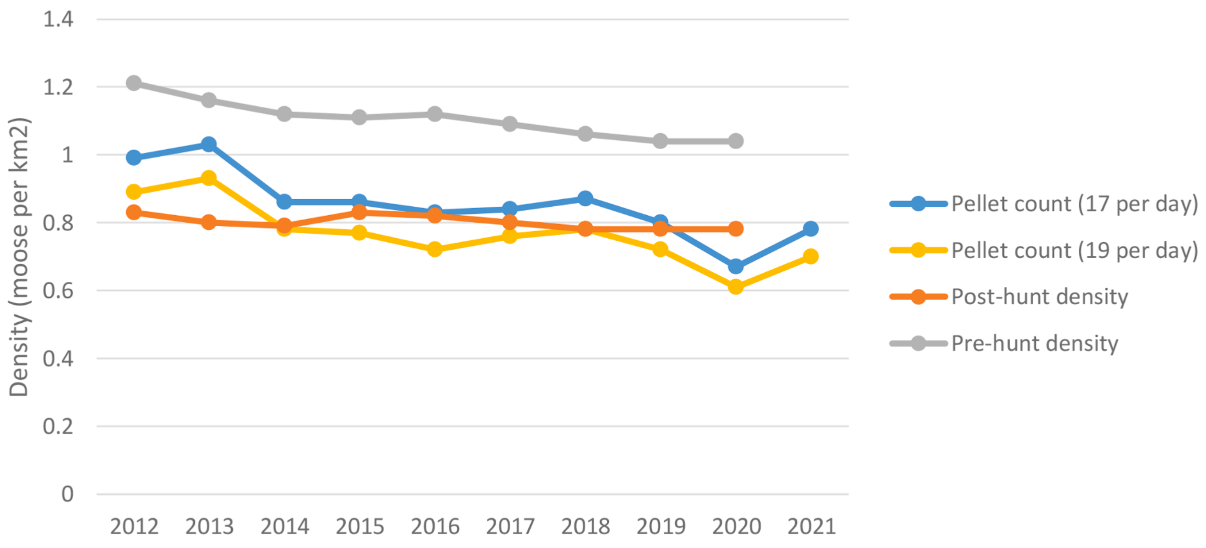

Fig. B.1. The trends of moose density in Jönköping county as estimated from moose pellet group count with two defecation rates (17 and 19 pellet groups per day), and estimated moose density from the model presented in the article. .

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Appendix C. Result of model estimate of population development between 2012 and 2020 within 20 counties

Table C.1 and Table C.2

Table C.1

Simulated post hunt moose population between 2012 and 2020 at different levels of other mortality.

County	Mortality	Year								
		2012	2013	2014	2015	2016	2017	2018	2019	2020
Stockholm	Low	3145	2940	2836	2702	2717	2613	2514	2420	2229
Stockholm	Middle	3274	3069	2960	2825	2831	2709	2585	2471	2269
Stockholm	High	3395	3188	3068	2917	2911	2789	2656	2523	2299
Uppsala	Low	5372	5445	5461	5381	5113	4681	4308	3884	3307
Uppsala	Middle	5584	5627	5604	5504	5226	4790	4388	3933	3338
Uppsala	High	5794	5845	5807	5679	5378	4910	4481	4009	3396
Södermanland	Low	3164	2941	2771	2719	2710	2566	2356	2275	2039
Södermanland	Middle	3279	3045	2882	2836	2832	2665	2431	2329	2079
Södermanland	High	3433	3231	3082	3052	3068	2932	2725	2652	2432
Östergötland	Low	5699	4941	4593	4422	4285	4180	4002	3860	3629
Östergötland	Middle	5909	5166	4831	4657	4491	4348	4135	3931	3620
Östergötland	High	6067	5301	4944	4725	4510	4324	4028	3738	3304
Jönköping	Low	7818	7461	7474	7784	7762	7574	7430	7535	7615
Jönköping	Middle	8162	7801	7789	8092	8023	7795	7598	7648	7639
Jönköping	High	8573	8278	8370	8743	8762	8601	8479	8624	8740
Kronoberg	Low	6732	6513	6303	6254	5985	5744	5541	5344	4893
Kronoberg	Middle	7042	6859	6687	6675	6461	6265	6087	5928	5524
Kronoberg	High	7336	7155	6993	6981	6738	6510	6317	6105	5621
Kalmar	Low	6004	5888	6047	6231	6036	5662	5490	5364	5107
Kalmar	Middle	6233	6119	6259	6418	6183	5727	5487	5301	4961
Kalmar	High	6593	6474	6603	6769	6556	6124	5891	5712	5366
Blekinge	Low	1456	1390	1314	1273	1251	1250	1271	1292	1325
Blekinge	Middle	1501	1423	1333	1282	1239	1219	1218	1227	1255
Blekinge	High	1561	1485	1407	1352	1311	1293	1298	1300	1315
Skåne	Low	1785	1741	1684	1652	1647	1668	1737	1793	1783
Skåne	Middle	1838	1801	1743	1723	1727	1758	1834	1897	1893
Skåne	High	2003	1983	1942	1927	1935	1964	2035	2089	2101
Halland	Low	3751	3368	3217	3198	3241	3163	3244	3381	3463
Halland	Middle	3933	3573	3455	3435	3469	3392	3490	3635	3707
Halland	High	4064	3700	3580	3573	3611	3525	3595	3712	3753
Västra_Götaland	Low	16,916	16,166	15,550	15,446	15,152	14,414	14,267	14,241	13,979
Västra_Götaland	Middle	17,655	16,940	16,340	16,205	15,779	14,911	14,620	14,465	14,005
Västra_Götaland	High	18,423	17,745	17,172	17,067	16,667	15,843	15,574	15,342	14,789
Värmland	Low	19,761	18,956	19,356	20,848	22,599	24,071	25,124	26,240	27,548
Värmland	Middle	20,279	19,420	19,697	21,027	22,562	23,764	24,510	25,286	26,143
Värmland	High	21,272	20,458	20,778	22,157	23,730	24,957	25,678	26,409	27,214
Örebro	Low	7703	7498	7264	7337	7580	7628	7748	7845	7831
Örebro	Middle	7944	7714	7474	7540	7765	7772	7824	7838	7723
Örebro	High	8264	8067	7847	7919	8116	8085	8104	8072	7879
Västmanland	Low	3963	3968	3926	3807	3703	3584	3406	3291	3098
Västmanland	Middle	4114	4082	4004	3848	3706	3546	3323	3168	2917
Västmanland	High	4291	4278	4226	4075	3944	3790	3559	3392	3138
Dalarna	Low	24,410	24,932	25,174	24,950	24,660	24,254	23,989	23,655	22,361
Dalarna	Middle	25,172	25,632	25,822	25,566	25,240	24,749	24,430	24,004	22,575
Dalarna	High	26,550	27,178	27,501	27,339	27,081	26,669	26,395	26,005	24,604
Gävleborg	Low	19,174	19,222	19,085	18,574	17,885	16,961	15,213	13,260	10,565
Gävleborg	Middle	19,712	19,780	19,673	19,173	18,487	17,540	15,741	13,691	10,909
Gävleborg	High	20,934	20,966	20,801	20,238	19,469	18,517	16,700	14,661	11,947
Västernorrland	Low	11,391	10,555	10,509	10,846	11,176	11,243	11,254	11,136	11,021
Västernorrland	Middle	11,867	11,024	10,981	11,349	11,714	11,816	11,875	11,795	11,726
Västernorrland	High	12,480	11,610	11,579	11,956	12,307	12,399	12,449	12,312	12,186

(*continued on next page*)

Table C.1 (*continued*)

County	Mortality	Year								
		2012	2013	2014	2015	2016	2017	2018	2019	2020
Jämtland	Low	44,326	43,572	44,005	45,114	45,982	46,112	45,438	45,078	44,214
Jämtland	Middle	46,275	45,537	45,970	47,010	47,859	48,042	47,370	46,998	46,045
Jämtland	High	47,685	46,801	47,037	47,824	48,282	47,963	46,620	45,421	43,420
Västerbotten	Low	33,060	32,011	32,525	32,801	32,446	30,834	29,427	28,057	25,551
Västerbotten	Middle	34,464	33,494	34,037	34,250	33,761	32,038	30,472	28,978	26,283
Västerbotten	High	35,665	34,654	35,155	35,309	34,629	32,551	30,567	28,483	25,220
Norrbotten	Low	31,663	31,598	31,368	30,756	30,213	29,106	28,520	28,138	26,894
Norrbotten	Middle	32,664	32,657	32,454	31,818	31,239	30,116	29,399	28,853	27,419
Norrbotten	High	34,499	34,553	34,383	33,813	33,251	32,088	31,282	30,624	29,059

Table C.2
Simulated post hunt moose density per km^2 between 2012 and 2020 at different levels of other mortality.

County	Mortality	Year								
		2012	2013	2014	2015	2016	2017	2018	2019	2020
Stockholm	Low	0.62	0.58	0.56	0.53	0.53	0.51	0.49	0.47	0.44
Stockholm	Middle	0.64	0.60	0.58	0.55	0.56	0.53	0.51	0.48	0.44
Stockholm	High	0.67	0.62	0.60	0.57	0.57	0.55	0.52	0.49	0.45
Uppsala	Low	0.58	0.59	0.59	0.58	0.55	0.51	0.47	0.42	0.36
Uppsala	Middle	0.60	0.61	0.61	0.59	0.56	0.52	0.47	0.42	0.36
Uppsala	High	0.63	0.63	0.63	0.61	0.58	0.53	0.48	0.43	0.37
Södermanland	Low	0.61	0.57	0.54	0.53	0.53	0.50	0.46	0.44	0.40
Södermanland	Middle	0.64	0.59	0.56	0.55	0.55	0.52	0.47	0.45	0.40
Södermanland	High	0.67	0.63	0.60	0.59	0.59	0.57	0.53	0.51	0.47
Östergötland	Low	0.61	0.53	0.49	0.48	0.46	0.45	0.43	0.42	0.39
Östergötland	Middle	0.64	0.56	0.52	0.50	0.48	0.47	0.45	0.42	0.39
Östergötland	High	0.65	0.57	0.53	0.51	0.49	0.47	0.43	0.40	0.36
Jönköping	Low	0.80	0.76	0.76	0.79	0.79	0.77	0.76	0.77	0.78
Jönköping	Middle	0.83	0.80	0.79	0.83	0.82	0.80	0.78	0.78	0.78
Jönköping	High	0.87	0.84	0.85	0.89	0.89	0.88	0.87	0.88	0.89
Kronoberg	Low	0.87	0.84	0.82	0.81	0.78	0.74	0.72	0.69	0.63
Kronoberg	Middle	0.91	0.89	0.87	0.86	0.84	0.81	0.79	0.77	0.72
Kronoberg	High	0.95	0.93	0.91	0.90	0.87	0.84	0.82	0.79	0.73
Kalmar	Low	0.59	0.58	0.60	0.62	0.60	0.56	0.54	0.53	0.51
Kalmar	Middle	0.62	0.61	0.62	0.63	0.61	0.57	0.54	0.52	0.49
Kalmar	High	0.65	0.64	0.65	0.67	0.65	0.61	0.58	0.57	0.53
Blekinge	Low	0.61	0.58	0.55	0.53	0.52	0.52	0.53	0.54	0.55
Blekinge	Middle	0.63	0.60	0.56	0.54	0.52	0.51	0.51	0.51	0.53
Blekinge	High	0.65	0.62	0.59	0.57	0.55	0.54	0.54	0.54	0.55
Skåne	Low	0.39	0.38	0.37	0.36	0.36	0.37	0.38	0.39	0.39
Skåne	Middle	0.41	0.40	0.38	0.38	0.38	0.39	0.40	0.42	0.42
Skåne	High	0.44	0.44	0.43	0.42	0.43	0.43	0.45	0.46	0.46
Halland	Low	0.81	0.73	0.69	0.69	0.70	0.68	0.70	0.73	0.75
Halland	Middle	0.85	0.77	0.74	0.74	0.75	0.73	0.75	0.78	0.80
Halland	High	0.88	0.80	0.77	0.77	0.78	0.76	0.77	0.80	0.81
Västra_Götaland	Low	0.57	0.54	0.52	0.52	0.51	0.48	0.48	0.48	0.47
Västra_Götaland	Middle	0.59	0.57	0.55	0.54	0.53	0.50	0.49	0.49	0.47
Västra_Götaland	High	0.62	0.60	0.58	0.57	0.56	0.53	0.52	0.52	0.50
Värmland	Low	1.21	1.16	1.19	1.28	1.39	1.48	1.54	1.61	1.69
Värmland	Middle	1.24	1.19	1.21	1.29	1.38	1.46	1.50	1.55	1.60
Värmland	High	1.31	1.26	1.27	1.36	1.46	1.53	1.58	1.62	1.67
Örebro	Low	0.88	0.86	0.83	0.84	0.87	0.88	0.89	0.90	0.90
Örebro	Middle	0.91	0.89	0.86	0.87	0.89	0.89	0.90	0.90	0.89
Örebro	High	0.95	0.93	0.90	0.91	0.93	0.93	0.93	0.93	0.90
Västmanland	Low	0.81	0.81	0.81	0.78	0.76	0.74	0.70	0.68	0.64
Västmanland	Middle	0.84	0.84	0.82	0.79	0.76	0.73	0.68	0.65	0.60
Västmanland	High	0.88	0.88	0.87	0.84	0.81	0.78	0.73	0.70	0.64
Dalarna	Low	0.90	0.92	0.92	0.92	0.91	0.89	0.88	0.87	0.82
Dalarna	Middle	0.92	0.94	0.95	0.94	0.93	0.91	0.90	0.88	0.83
Dalarna	High	0.98	1.00	1.01	1.00	0.99	0.98	0.97	0.96	0.90
Gävleborg	Low	0.98	0.99	0.98	0.95	0.92	0.87	0.78	0.68	0.54
Gävleborg	Middle	1.01	1.01	1.01	0.98	0.95	0.90	0.81	0.70	0.56

(*continued on next page*)

Table C.2 (*continued*)

County	Mortality	Year 2012	2013	2014	2015	2016	2017	2018	2019	2020
Gävleborg	High	1.07	1.08	1.07	1.04	1.00	0.95	0.86	0.75	0.61
Västernorrland	Low	1.05	0.97	0.97	1.00	1.03	1.03	1.04	1.02	1.01
Västernorrland	Middle	1.09	1.01	1.01	1.04	1.08	1.09	1.09	1.09	1.08
Västernorrland	High	1.15	1.07	1.07	1.10	1.13	1.14	1.15	1.13	1.12
Jämtland	Low	0.79	0.78	0.79	0.81	0.82	0.82	0.81	0.81	0.79
Jämtland	Middle	0.83	0.81	0.82	0.84	0.86	0.86	0.85	0.84	0.82
Jämtland	High	0.85	0.84	0.84	0.85	0.86	0.86	0.83	0.81	0.78
Västerbotten	Low	0.61	0.59	0.60	0.61	0.60	0.57	0.54	0.52	0.47
Västerbotten	Middle	0.64	0.62	0.63	0.63	0.62	0.59	0.56	0.54	0.49
Västerbotten	High	0.66	0.64	0.65	0.65	0.64	0.60	0.57	0.53	0.47
Norrbotten	Low	0.40	0.40	0.40	0.39	0.38	0.37	0.36	0.36	0.34
Norrbotten	Middle	0.41	0.41	0.41	0.40	0.40	0.38	0.37	0.37	0.35
Norrbotten	High	0.44	0.44	0.44	0.43	0.42	0.41	0.40	0.39	0.37

Appendix D. Description of population routine to estimate initial population

During the model's initialization, an estimated total population is calculated that meets the required parameters for adult sex ratio, calf birth sex ratio, net recruitment rate, and male proportion in the harvest. The population model used in step 2 is fairly similar to this one (see article Section 2.4). The primary distinction is that in the latter model, the harvest of bulls, females, and calves is used, rather than the population being a function of harvest.

Hunting

Hunting is applied iteratively within a goal seeking algorithm that aims to meet a specified population density at steady state. In other words, a hunting pressure (see chapter 4) change annually until the wanted steady state population is met. The model runs 2000 annual cycles to ensure that a steady state density is reached. The model is initialised with an arbitrary population. In addition to setting wanted density, the algorithm also adjusts adult sex-ratio to a desired ratio. The demographic structure of the population is determined by the adult sex-ratio and a certain proportion of calves in the harvest.

Hunting of adult females

The hunted (H) females (f) in age-class i is calculated using an expression where a coefficient (h) is allowed to vary iteratively between each annual cycle to find a stable population equilibrium that meets the wanted density.

$$H_{f,i} = h(1-\gamma aF_i) \times S_{f,i} \tag{1}$$

where F is age-specific fecundity and a is the parameter used in Eq. (4) (original paper) and γ (0.5) is a constant that scales the fecundity-dependent hunting pressure. In this way, hunting is allocated more to females with a lower fecundity rate. The theory behind this is that females that are followed by one or more calves have a lesser risk of being shot. Younger and older females thereby have a higher risk of being harvested. Setting of h is described further in Section 4, this appendix.

The post hunt female winter population (W) is calculated by subtracting the harvested females from the pre-hunt summer population.

$$W_f = \sum \left(S_{f,i} - H_{f,i}\right) \tag{2}$$

The pre-hunt male population (S_m) is calculated by subtracting the adult females from the total pre-hunt population.

$$S_m = S_t - S_f \tag{3}$$

The total post-hunt adult population (W_t) is estimated by using the wanted proportion of adult males (p).

$$W_t = \frac{W_f}{(1-p)} \tag{4}$$

The post-hunt adult male population (W_m) is then estimated by subtracting the adult females from the total adult population. Note that this is an estimated recursive value that later is corrected.

$$W_m = W_t - W_f \tag{5}$$

Male hunting

Hunting of males is calculated by summing the proportion of each age class multiplied by the difference between pre-hunt male population and the estimated post-hunt male population.

$$H_{m,i} = \frac{S_{m,i}(S_m - W_m)}{S_m} \tag{6}$$

The post-hunt adult population is then calculated by subtracting the hunted individuals from the pre-hunt population. This is the corrected value of post-hunt winter population of males.

$$W_{m,i} = S_{m,i} - H_{m,i} \tag{7}$$

Births

The number of born calves (B) is a calculated from age specific (i) fecundity (F) (Eq. (4) in the main article) and number of females (W_f) in each cohort in winter.

$$B = \sum F_i W_f \tag{8}$$

A sex ratio divides the total number of births into females and males.

Mortality

Mortality is calculated twice a year. First in spring after the winter period (winter mortality). Second, before hunting period starts in the autumn (summer mortality).

The number of dead adults

In the model, adult mortality is set for each sex. However, the mortality function is not only specific for each sex but also for each age class. To implement the sex-specific net mortality, a correction factor needs to be calculated before applying sex- and age-specific adult mortality. This is performed by the following two equations. First, mortality (σ) is calculated with age specific mortality (m) derived from a mortality function (Eq. (5) in the main article).

$$\sigma_s = \sum \frac{m_{s,i} S_{s,i}}{3} \tag{9}$$

A correction factor (k) is then calculated for each sex (s).

$$k_s = \frac{M_s \sum S_{s,i}}{3\sigma_s} \tag{10}$$

where M is the given total mortality rate for sex, S is summer population and i is age-class.

It is assumed that all adults have the same risk of being killed by carnivores or traffic incidents. A ratio (r) is calculated to separate carnivore- and traffic related mortality into the two sexes.

$$r_s = \frac{\sum S_{s,i}}{\sum S_i} \tag{11}$$

The total number of dead adults (D) in summer for a specific sex and age class can now be calculated.

$$D_{s,i} = \frac{k_s M_{s,i} S_{s,i}}{3} + \frac{0.1 * r_s m_w S_{s,i}}{3 \sum S_{s,i}} + \frac{r_s m_t S_{s,i}}{3 \sum S_{s,i}} \tag{12}$$

where m is the number of individuals killed by wolves (w) and traffic (t). Note that bears (b) are assumed to only kill calves. It is further assumed that 10% of the total wolf kills is on adults during summer and the rest is attributed to calves. Further, the equation described here constitute mortality for four summer months (i.e. 1/3 of the total annual mortality). In winter it is assumed that 20% of wolf kills is attributed to adults.

Calf mortality

The number of dead calves (D_0) (age-class 0) in summer for each sex is calculated in a simpler fashion.

$$D_{s,0} = R_s M_{s,0} B_{s,0} + \frac{0.9 R_s m_w}{3} + \frac{R_s m_b}{3} + \frac{R_s m_t}{3} \tag{13}$$

where R is the proportion of the specific sex at birth (e.g. female calves/calves), M *is the* summer calf mortality rate for sex s, B is the number of births. Calculation of calf winter mortality is similar except for that 80% of the wolf kills is attributed to calves, no calves is killed by bears (b) during winter and that winter mortality is 2/3 of the total annual mortality. The mortality rate (M), related to other mortality, can be set specifically for summer and winter to allow for difference in calf mortality during these two seasons.

Automatic hunting device

Algorithm

The automatic hunting device is an algorithm that seeks a target steady state population by iteratively applying a certain hunting pressure. The fecundity constant (a in Eq. (4), main article) is held constant during this process. During step 1 (chapter 2.3), an overarching algorithm sets the value of a and the initial population by iteratively seeking a specific net recruitment rate and harvest rate. The algorithm finds a level of a and initial population where harvest and recruitment rate (calves per female after summer mortality) corresponds to the actual data for that particular hunting area. In this section, the algorithm that finds a specific harvest that will keep the population at a specified wanted density, is described.

Algorithm

1. Parameters are set
   a. Wanted density,
   b. Wanted pre-hunt proportion of bulls in the adult population.
   c. Proportion of calves in total harvest,
   d. Calf-sex ratio
   e. Mortality not related to hunting
2. Run the population iteratively for a number of times (2000) where hunting pressure is applied to the annual harvest. The algorithm seeks the hunting pressure that results in the wanted steady state density. To speed up this process the use of numerically solving differential equations is used.
3. The algorithm ends when a steady state of wanted density is met.

Numerically solving of differential equations

Determining hunting pressure is performed in each iteration by the use of two variables that are updated within this procedure. The first variable (p) follows the population density. The second variable is used to set the hunting pressure (h). Heun's algorithm is used to numerically solve a first order differential equation. Heun's method is a little bit more advanced than the more common Euler's method. Both of these methods use the idea of local linearity or linear approximation. The difference between Euler's method and Heun's method is that the latter use a predictor and then a corrector to calculate the slope. The slope is then the average of the predictor and the correction. The method is in other word recursive and a bit more efficient that Euler's method.

Variable p

A population density variable (P) is that follow the simulated population is used. The slope of population density is a function of present density (D) derived from the population model and current value of p.

$$\frac{dP}{dt} = D - P \tag{14}$$

Variable p is then updated using the Heun's algorithm (not described here) and timestep s (0.25).

$$P_{t+1} = P_t + \frac{dP}{dt}s \tag{15}$$

Variable h

The current population trend (T) is first calculated. If the simulated population is below P, the trend is negative.

$$T = \frac{D - P}{P} \tag{16}$$

The deviance (H) from wanted density (w) is calculated, where k_1 is a constant setting sensitivity (0.01).

$$H = \min\left(0.2, k_1(P - w)^3\right) \tag{17}$$

Finally, the slope for the hunting pressure (h) is calculated by adding T and H.

$$\frac{dh}{dt} = H + T \tag{18}$$

Variable h is updated in the same way as for variable P.

$$h_{t+1} = h_t + \frac{dh}{dt}s \tag{19}$$

Variable h is then used in Eq. (1) (this appendix) to set the annual hunting pressure on females.

Appendix E. Parameters

Table E.1

Table E.1
Summary of mortality used in the model.

Category	Variable	Specifics	Refs.
Carnivores:			
- **Bear kills**	6 calves per adult bear	Only summer predation	Rauset et al. (2012)
- **Wolf kills**	120 moose per year	Summer: 90% calves, 10% adults. Winter: 80% calves, 20% adults.	Zimmerman et al. (2014), Sand et al. (2005, 2008)
Traffic	Traffic related mortality	1/3 in the summer, 2/3 in winter	www.älgdata.se, www.viltolycka.se
'Other mortality'			Lorentsen et al. (1991), Saether et al. (1996), Stubsjøen et al. (2000), Swenson et al. (2001), Ericsson et al. (2001), Ericsson and Wallin (2001), Broman et al. (2002), Solberg et al. (2003), Gundersen (2003), Rönnegård et al. (2008)
- **Calves**	3–10%	1/3 in the summer, 2/3 in winter	
- **Adults**	2–4%	"	
Harvest	Annual hunting statistics	Bulls, cows, bullcalves, cowcalves	www.älgdata.se

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