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ARTICLE

No Allee effect detected during the natural recolonization by a large carnivore despite low growth rate

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Abstract

Eurasian lynx (*Lynx lynx*) have recently naturally recolonized southern Sweden. The first documented reproduction of lynx in recent times occurred in 2003, and the population increased from 2 to 48 family groups (the unit of measurement in Swedish monitoring) during its first 18 years (2003/2004–2020/2021). We did not detect any Allee effect, that is, lower growth rate at low population density, during the recolonization of southern Sweden, although our population simulations revealed a non-negligible (30%) chance that population observed development could include an Allee effect. The probable absence of an Allee effect was likely because colonizing females did not lack mating partners, as a larger number of wide-ranging males were established in the area before documented reproduction took place. Despite the absence of an Allee effect, the growth rate during recolonization was lower in southern Sweden ($\lambda = 1.20$) than in central Sweden ($\lambda = 1.29$). We have no evidence of higher mortality, including that from poaching, or lower reproduction in southern Sweden could explain the lower growth rate. Instead, we suggest that the lower growth rate during the recolonization of southern Sweden was explained by fewer immigrants arriving from central Sweden due to areas of less suitable habitat between central and southern Sweden, partially preventing immigration southward. From a conservation point of view, it is positive that this small population could recover without being negatively influenced by an Allee effect, as small populations with an Allee effect experience lower viability than those without.

KEYWORDS
Allee effect, barrier, colonization, growth rate, habitat suitability, inverse density dependence, lynx

INTRODUCTION

For populations to successfully recolonize areas where they were previously extirpated, several requirements should be met during the colonization process (Ferriere et al., 2000; Sutherland et al., 2000; Whitmee & Orme, 2013). First, there must be a source population from which individuals can disperse. Second, there needs to be suitable habitat where dispersing individuals can establish. Third, dispersing individuals should be able to move through the interim landscape, thus enabling connectivity between suitable areas that are not too far apart and not separated by dispersal barriers (With et al., 1997). However, anthropogenic barriers, such as roads, can reduce connectivity between suitable areas, or landscape permeability, when individuals are killed in vehicle collisions (Kramer-Schadt et al., 2004; Stoner et al., 2013). Finally, even though immigration enables successful colonization, it is vital that the population growth rate remains positive, to maintain itself and to expand. During the early phase of colonization, population sizes are naturally small. The Allee effect (i.e., inverse or positive density dependence) is a situation in which the density and growth rate of a small population are positively correlated; that is, the population growth rate increases as the population density increases (Courchamp et al., 1999). The Allee effect can have a strong influence on the probability of successful colonization, as there could be a threshold in population size below which a population has a very slow or even negative growth rate, known as the Allee threshold. Three main factors that may cause Allee effects are inbreeding, demographic stochasticity, and cooperative interactions (Courchamp et al., 1999; Lande, 1998). Within the last category, a key factor is the ability to find mates, which can be difficult at low population densities when animals are far apart, even for nonsocial species (Gascoigne et al., 2009; Wells et al., 1998). There are few documentations of Allee effects in large solitary carnivores (Gregory et al., 2010), probably because it is very difficult to detect an Allee effect in decreasing populations (Gilroy et al., 2012; Molnar et al., 2008). Therefore, predictive process-based models are often used to forecast potential risks of Allee effects (Molnar et al., 2014). Courchamp et al. (2000) showed using mechanistic models that pack formation, that is, the probability to colonize new territories, could lead to Allee effect in African wild dogs (*Lycaon pictus*), which are obligate cooperative breeders. For a solitary predator, polar bears (*Ursus maritimus*), Molnar et al. (2014) used process-based models and showed the mate finding at low density could cause an Allee effect. In an increasing wolf (*Canis lupus*) population in southern Scandinavia, Wikenros et al. (2021) found that the age of first reproduction in females decreased with increasing population size, which indicates an Allee effect. In this study, we explored whether an Allee effect influenced a recent increase in the population of a solitary predator, the Eurasian lynx (*Lynx lynx*), recolonizing southern Sweden.

The Eurasian lynx population in Sweden was severely reduced during the 19th and early 20th centuries due to human persecution, encouraged by government bounties up until 1928. At that time, possibly less than 100 lynx remained in the country, in one or two isolated populations in central Sweden. Since then, lynx have naturally spread southward and have now recolonized almost all of Sweden. In the winter 2021, the national population was estimated to be about 1000–1400 individuals (Frank & Tovmo, 2021) with limited hunting of lynx permitted based on yearly regional population estimates (Andrén et al., 2020). Southern Sweden was the last area to be recolonized, and the first documented reproduction of lynx in this area in modern times occurred in 2003 (Wildlife Damage Center, 2005). Since then, the lynx population in this area has continued to increase (Frank & Tovmo, 2021; Liberg & Andrén, 2006, and Figure 1).

There are large areas of suitable habitat for lynx in southern Sweden (Hemmingmoore et al., 2020). However, areas between central and southern Sweden are of lower habitat suitability, with highways, railways, agricultural land, three large lakes, and densely human-populated areas, which may partially isolate southern from central Sweden (Hemmingmoore et al., 2020). To what extent this area acts as a barrier is still unknown. Although it has a lower habitat suitability, the area spans a relatively short distance in terms of lynx movement capability and there are several documented cases of lynx dispersing between central and southern Sweden (Samelius et al., 2012).

The recolonization of Sweden occurred in phases, with the lynx population establishing in central Sweden in progressively southward waves prior to the recolonization of southern Sweden at a later time (Liberg & Andrén, 2006, Figures 1 and 2). It can therefore be considered as two separate colonization events. Thus, our aims are (1) to test whether lynx recolonization in southern Sweden (18-year-long data set) was affected by an Allee effect (i.e., inverse or positive density-dependent growth rate) and (2) to compare the lynx population growth rate during the recolonization of southern Sweden with that of central Sweden. In the comparison between southern and central Sweden, we also explored the effects of traffic mortality by adding lynx killed in vehicle collisions to the models together with the legal harvest.

STUDY AREA

The main study area was southern Sweden (approximately 73,000 km^2) south of the large agricultural areas in the counties of Västra Götaland and Östergötland (Figure 1). It is dominated by forest (63%), most of which is intensively managed with the primary tree species being not only Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but also birch (*Betula pubescens*

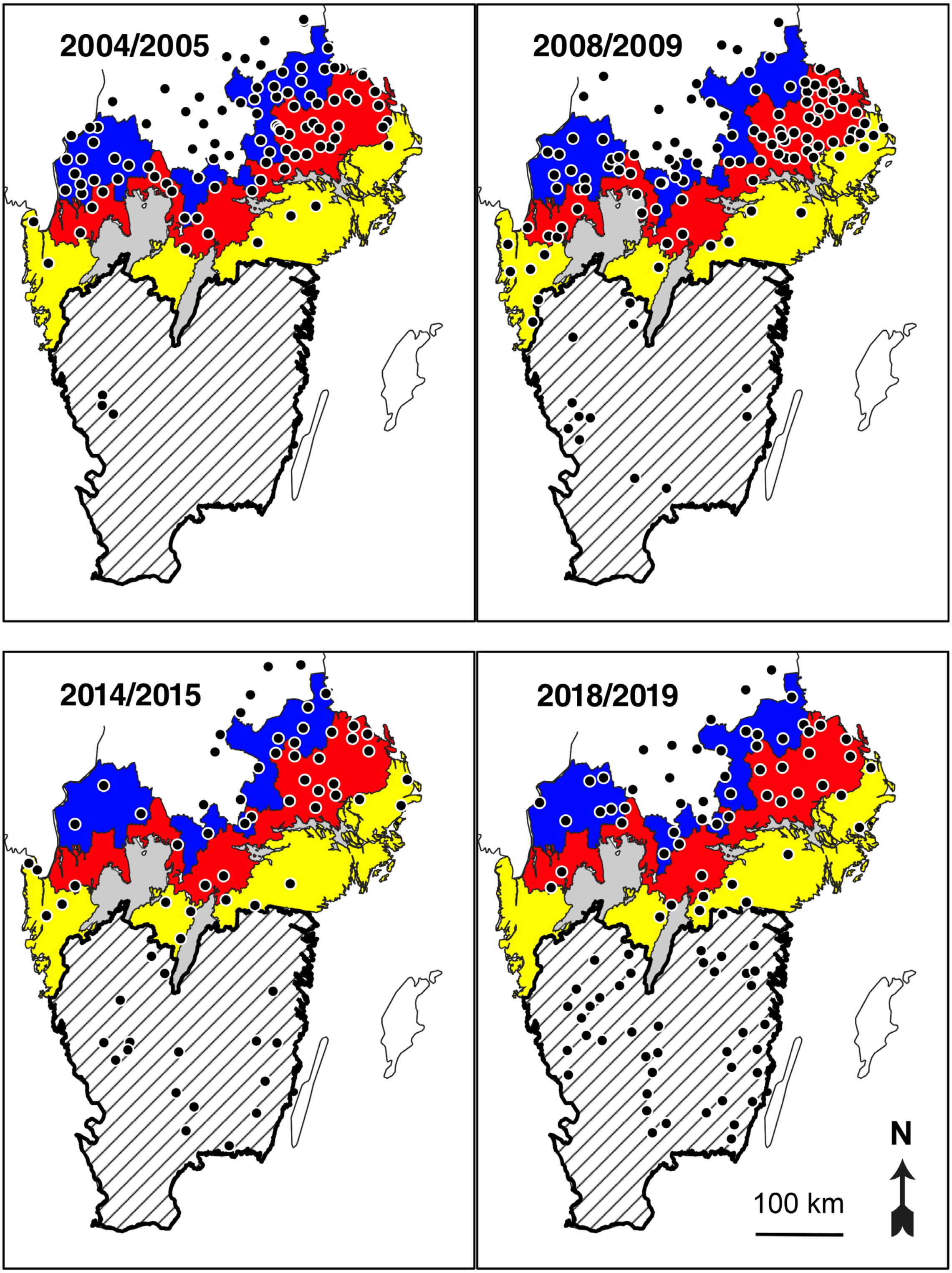

FIGURE 1 Distribution of lynx family groups (black dots) documented in central Sweden (Region A [blue], Region B [red], and Region C [yellow]) and southern Sweden (striped) in winter 2004/2005, 2008/2009, 2014/2015, and 2018/2019. The area north of Region A (white) was not included in the study

and *Betula pendula*), and interspersed with other broad-leaved species such as aspen (*Populus tremula*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), lime (*Tilia cordata*), oak (*Quercus robur*), and beech (*Fagus sylvatica*) (Esseen et al., 1997). Agricultural and grasslands cover about 24% of the region. Southern Sweden is partly isolated from central Sweden by highways, railways, agricultural land, three large lakes, and densely human-

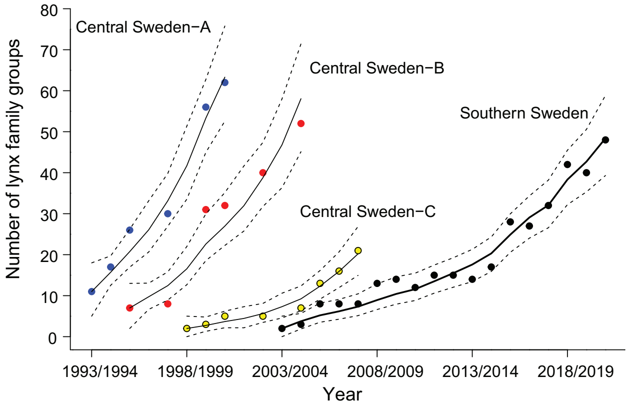

FIGURE 2 Number of lynx family groups in relation to year in central Sweden (Region A [blue dots], Region B [red dots], and Region C [yellow dots]) and southern Sweden (black dots). Medians of posterior distributions of the estimated number of lynx family groups (solid line) and 95% Bayesian credible intervals (dashed lines). See Appendix S1: Figure S7 for log(number of lynx family groups) in relation to year

populated areas (Hemmingmoore et al., 2020). The mean primary paved road density is 0.47 km/km^2, and the mean secondary gravel road density is 1.52 km/km^2.

We divided central Sweden (north of the main study area) into three regions (A, B, and C, total area approximately 65,000 km^2) to describe the frontiers of recolonization as the population progressed southward (Figure 1). These three areas are parts of the southern continuous boreal forest. Forest covers 69%, and most of it is intensively managed and dominated by Norway spruce and Scots pine. Agricultural land covers 24% of the land and increases toward the south. The mean primary road density is 0.39 km/km^2, and the mean secondary road density is 1.18 km/km^2.

MATERIALS AND METHODS

Lynx monitoring

We used data from the Swedish lynx monitoring system, available in the official carnivore database (Rovbase; rovbase30.miljodirektoratet.no). Lynx monitoring in Sweden is based on non-replicated counts of family groups (Gervasi et al., 2013; Linnell, Fiske, et al., 2007; Linnell, Odden, et al., 2007). The monitoring is primarily conducted from December to the end of February and largely based on snow-tracking and identifying lynx tracks from two or more individuals, which are then assessed as a family group consisting of an adult female and young of the year (Linnell, Odden, et al., 2007). Simultaneous snow tracking or a distance criterion based on home-range sizes and movement patterns from radiomarked female lynx with kittens is used to separate observations of different family groups, to assure that counts of family groups are distinct (Gervasi et al., 2013; Linnell, Odden, et al., 2007). Additional observations that are used to confirm reproduction include camera-trap images of kittens, and any kittens shot in the early part of the hunting season (February) or killed in traffic accidents. Trained and authorized personnel from the Swedish County Administration Boards perform the lynx monitoring. Game wardens, hunters, and the public can report records of lynx tracks, but all observations need to be verified by the authorized personnel before being confirmed and entered into the carnivore database and thus used in the national count of family groups. The family group counts are multiplied by a conversion factor to encompass the entire lynx population, including males and nonreproducing females. The conversion factor is on average 5.48 (±0.40 SD) in central and southern Sweden (Andrén et al., 2002). There was a good fit between the monitored number of lynx family groups and the reconstructed population size (Nilsen et al., 2011). Thus, the lynx monitoring provides a proxy of all lynx in an area. In the population models, we included dead lynx. Data on dead lynx were downloaded from the carnivore database (Rovbase; rovbase30.miljodirektoratet.no).

Population model

We used the Bayesian hierarchical population models to estimate the posterior distribution of the unobserved lynx population size, using four different process equations to assess the presence of an Allee effect during lynx colonization of southern Sweden. In all process models, μ_t is the deterministic prediction of the lynx population at time t, N_t is the unobserved population size at time t, $H_{(t-1)}$ is the observed legal harvest of lynx at time $t-1$ (i.e., legal harvest from the previous hunting season in February and March), and σ_{proc} is the SD of the unobserved population size.

Process model 1—Linear density-dependent growth rate

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp\left(a_0 + a_1 \times N_{(t-1)}\right)\right]$$

$$N_t \sim \text{lognormal}\left(\mu_t, \sigma_{\text{proc}}\right)$$

Here, a_0 represents the growth rate ($\log(\lambda)$) at zero density, and a_1, the per capita change in growth rate. An

Allee effect would result in a positive a_1 estimate ($a_1 > 0$), while for classic density dependence, the a_1 estimate would be negative ($a_1 < 0$). This model describes the same linear relationship between growth rate and population density over the entire range of the data. If $a_1 > 0$, the growth rate increases continuously with population density; that is, population density never reaches the point where the relationship between growth rate and population density changes from being positive to negative (Appendix S2: Figure S2).

Process model 2—Quadratic density-dependent growth rate

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp\left(b_0 + b_1 \times N_{(t-1)} + b_2 \times {N_{(t-1)}}^2\right)\right]$$

$$N_t \sim \mathrm{lognormal}\left(\mu_t, \sigma_{\mathrm{proc}}\right)$$

Here, b_0 represents the growth rate ($\log(\lambda)$) at zero density, and b_1 and b_2 describe the shape of the quadratic curve. We added the quadratic term to test whether the growth rate was first positive at low densities (i.e., Allee effect), and then changes to negative when density increases (i.e., classic density dependence), resulting in a hump-shaped or concave growth rate curve, resulting in a negative b_2 estimate ($b_2 < 0$). This hump-shaped relationship between growth rate and population density means that the population density reaches the point where the relationship between growth rate and population density changes from being positive to negative (Appendix S2: Figure S2).

Process model 3—Density-independent growth rate and comparing between southern and central Sweden

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp(c_0)\right]$$

$$N_t \sim \mathrm{lognormal}\left(\mu_t, \sigma_{\mathrm{proc}}\right)$$

Here, c_0 represents the estimated constant density-independent growth rate ($\log(\lambda)$). We used one model to estimate the density-independent growth rate and included two region-specific growth rates in the model: $c_{0-\mathrm{southern}}$ (for southern Sweden) and $c_{0-\mathrm{central}}$ (one common for regions A, B, and C in central Sweden), which is expected to decrease uncertainty due to borrowing strength between data sets (Hobbs & Hooten, 2015; see also Appendix S1: Table S1 and Figure S1). We estimated one common growth rate across the three regions of central Sweden because the data show a similar rate during each wave of recolonization, and also due to small sample sizes within each region and because the recolonization of central Sweden occurred within continuous suitable lynx habitat (Hemmingmoore et al., 2020).

Process model 4—Density-independent growth rate, including lynx killed in vehicle collisions and comparing between southern and central Sweden

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)} - T1_{(t-1)}\right) \times \exp(d_0) - T2_{(t-1)}\right]$$

$$N_t \sim \mathrm{lognormal}\left(\mu_t, \sigma_{\mathrm{proc}}\right)$$

Here, d_0 represents the estimated constant density-independent growth rate when lynx killed in vehicle collisions (T) are included in the yearly mortality estimate, along with legal harvest. We used one model to estimate the density-independent growth rate, including lynx killed in vehicle collisions, and included two region-specific growth rates in the model: $d_{0-\mathrm{southern}}$ (for southern Sweden) and $d_{0-\mathrm{central}}$ (one common for regions A, B, and C in central Sweden). $T1_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the census in February but before the birth pulse in late May at time $t-1$, and $T2_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the birth pulse in late May but before the census in February at time t.

Observation model

All four process equations were linked to data using the same observation equation:

$$\mathrm{alpha}_t = {N_t}^2 / \sigma^2_{\mathrm{Nobs}}$$

$$\mathrm{beta}_t = N_t / \sigma^2_{\mathrm{Nobs}}$$

$$\varphi_t \sim \mathrm{gamma}(\mathrm{alpha}_t, \mathrm{beta}_t)$$

$$Fgobs_t \sim \mathrm{Poisson}(p \times \varphi_t)$$

where $Fgobs_t$ is the observed number of family groups at time t, p is the number of family groups per total number of lynx, and ${\sigma^2}_{\text{Nobs}}$ is the estimated observation error of the population size. This formulation views the count data hierarchically, where the mean observed count of lynx family groups at time t is Poisson-distributed with mean φ_t multiplied by p, and this mean (φ_t) is drawn from a gamma distribution with a mean equal to the prediction of the process model (N_t) and a SD for observation error (σ_{Nobs}). The shape parameters for the gamma distribution (alpha$_t$ and beta$_t$) were derived from N_t and ${\sigma^2}_{\text{Nobs}}$ using moment matching. We chose this approach because it allows the uncertainty in the data model to be larger than the variance of the Poisson parameter φ_t. This gamma–Poisson mixture for count data is the same as using a negative binomial distribution, but has computational advantages (McCarthy, 2007).

Model fitting and evaluation

Vague prior distributions were assigned to: a_0, a_1, b_0, b_1, b_2, c_0, and d_0, $\sim$ normal(0, 100), $\sigma_{\text{proc}} \sim$ uniform(0, 10), and $\sigma_{\text{Nobs}} \sim$ uniform(0, 100). On average, one lynx family group represents 0.184 ± 0.013 SD of total number of lynx in the population (Andrén et al., 2002). The prior for the number of family groups per total number of lynx (p) was calculated from this using moment matching; $p \sim$ beta(152, 677). We approximated the marginal posterior distributions of parameters fitting the models to data using the Markov chain Monte Carlo algorithm implemented in *rjags* and *coda* packages (Plummer, 2003) in R (R Core Team, 2018). We ran three chains of 100,000 iterations following a 50,000 burn-in. Convergence was checked by visual inspection of trace plots and by the diagnostics of Heidelberger (Heidelberger & Welch, 1983) and Gelman (using the threshold value of <1.02 indicating very low variation between the three chains; Brooks & Gelman, 1997) implemented in the *coda* package (Plummer, 2003). We used posterior predictive checks to evaluate the lack of fit between models and data using the Bayesian p values (p value >0.1 or <0.9 suggests a good fit between the model and the data; Hobbs & Hooten, 2015). We present posterior means and SD with the associated 95% Bayesian credible intervals (BCIs).

We used leave-one-out cross-validation to compare the models and estimated the mean square prediction error (MSPE). Low values of MSPE indicate models with a greater predictive ability (Hobbs & Hooten, 2015).

Statistical power analyses

We performed statistical power analyses by comparing the posterior distributions for the coefficients estimated from the monitoring data with the coefficients estimated from simulated data of a population development with Allee effect (i.e., Model 1 with positive linear density-dependent growth rate; Model 2 with negative quadratic density-dependent growth rate), as well as density-independent growth rate (Model 3). First, we used deterministic models to generate expected parameter values. Second, we generated stochastic population development by randomly selecting values for the model parameters (i.e., a_0 and a_1 for Model 1; b_0, b_1, and b_2 for Model 2; and c_0 for Model 3). These parameter values were randomly drawn from a normal distribution (Appendix S2: Table S1). Finally, we made 1000 simulations of the population development for each model, using the Bayesian hierarchical population models (process and observation models) described above to estimate the posterior distribution of each parameter. The model parameters from these simulations were then compared with the parameters estimated from the monitoring data. These comparisons give an indication of the probability to detect a linear density-dependent growth rate (difference for a_1 estimates) or a negative quadratic density-dependent growth rate (difference for b_2 estimates), given the observed monitoring data. See Appendix S2 for a detailed description of the statistical power analyses.

RESULTS

Model 1—Linear density-dependent growth rate

The mean coefficient estimate for the density dependence of the growth rate was negative ($a_1 = -0.00082$; Table 1), and there was only a 14% probability that the coefficient would be positive ($a_1 > 0$), thus contributing positively to the population growth rate as predicted from an Allee effect. The estimates of a_0 and a_1 passed both the Heidelberger and Gelman diagnostics. The Bayesian p value was 0.27, suggesting a good fit between the model and the data. However, the results were sensitive to the initial condition (i.e., 2 lynx family groups observed in winter 2002/2004), probably because the increase from 2 (2003/2004) to 3 (2004/2005) lynx family groups in the data set results in a high deterministic growth rate ($\lambda = 1.5$ or $\log(\lambda) = 0.41$). When changing the initial condition to 3 or 4 family groups, the a_1 estimate was closer to zero (27% and 45% probability for a positive a_1, respectively; Appendix S1: Table S2). The Bayesian p values were 0.22 and 0.20 for these alternative models. Consequently, from the posterior distribution there is neither a support for a positive (Allee effect) nor a negative (classic density dependence) relationship between growth rate and population density, because a_1 (per capita change in

TABLE 1 Statistics summarizing posterior distributions (mean ± SD) of the population model parameters estimates, with the associated 95% Bayesian credible intervals (BCIs)

Parameter	Definition	Mean ± SD	95% BCI
Model 1—Linear density-dependent growth rate			
a_0	Growth rate at zero density on log scale	0.264 ± 0.101	0.0970 to 0.503
a_1	Density-dependent effect on growth rate on log scale	−0.00082 ± 0.00090	−0.0029 to 0.00070
p	Number of family groups per total number of lynx	0.183 ± 0.0132	0.158 to 0.210
σ_{proc}	Process SD on log scale	0.163 ± 0.094	0.0129 to 0.377
σ_{Nobs}	Estimated observation error of the population size	6.43 ± 5.08	0.263 to 19.0
Model 2—Quadratic density-dependent growth rate (priors ~ uniform(−4, 4))			
b_0	Growth rate at zero density on log scale	0.499 ± 0.241	0.119 to 1.085
b_1	Describes the shape of the quadratic curve	−0.00646 ± 0.00517	−0.0191 to 0.0020
b_2	Describes the shape of the quadratic curve	0.000026 ± 0.000024	−0.000012 to 0.000083
p	Number of family groups per total number of lynx	0.186 ± 0.0135	0.160 to 0.213
σ_{proc}	Process SD on log scale	0.163 ± 0.099	0.0121 to 0.390
σ_{Nobs}	Estimated observation error of the population size	6.45 ± 5.33	0.236 to 19.7
Model 3—Density-independent growth rate and comparing between southern and central Sweden			
$c_{0-\text{southern}}$	Density-independent growth rate on log scale in southern Sweden	0.179 ± 0.0262	0.128 to 0.237
$c_{0-central}$	Density-independent growth rate on log scale central Sweden	0.253 ± 0.0241	0.205 to 0.304
p	Number of family groups per total number of lynx	0.185 ± 0.0134	0.159 to 0.211
σ_{proc}	Process SD on log scale	0.0771 ± 0.0557	0.00212 to 0.203
σ_{Nobs}	Estimated observation error of the population size	4.27 ± 3.43	0.093 to 12.7
Model 4—Density-independent growth rate, including lynx killed in vehicle collisions and comparing between southern and central Sweden			
$d_{0-\text{southern}}$	Density-independent growth rate on log scale in southern Sweden	0.207 ± 0.0249	0.159 to 0.262
$d_{0-\text{central}}$	Density-independent growth rate on log scale in central Sweden	0.269 ± 0.0231	0.223 to 0.317
p	Number of family groups per total number of lynx	0.184 ± 0.0137	0.157 to 0.211
σ_{proc}	Process SD on log scale	0.0716 ± 0.0516	0.00293 to 0.191
σ_{Nobs}	Estimated observation error of the population size	4.37 ± 3.40	0.157 to 12.7

Note: See Appendix S1: Figures S2–S6 for posterior and prior distributions of the parameters.

growth rate) largely overlapped zero and showed good convergence around zero.

From the statistical power analysis, parameter a_1 estimated from our monitoring data was closer to zero and had a negative mean value, compared with the positive mean a_1 from the simulated data (Appendix S2: Figure S4). There was a 71% probability that a_1 from the monitoring data would be smaller than a_1 from the simulations (Appendix S2: Figure S5). Thus, about 30% of the simulated population development with a known Allee effect could be similar to the observed population development in our study.

Model 2—Quadratic density-dependent growth rate

The posterior distributions for all three (b_0, b_1, and b_2) coefficients were centered around zero with large SDs (Appendix S1: Figure S3), and they did not pass Heidelberger diagnostics. As the posterior distributions for b_0, b_1, and b_2 were close to the priors (Appendix S1: Figure S3), we also tested more informative priors restricting their range to more biological relevant values (~uniform(−4, 4)). Using restricted priors, all coefficients converged (Table 1), with a 99% probability for b_0 to be positive, a 92% probability for b_1 to be negative, and an 89% probability for b_2 to be positive. However, the coefficients resulted in a convex relationship between growth rate and population density (i.e., first decreasing and then increasing growth rate with increasing density). The Bayesian p value was 0.32, and the coefficient estimates passed the Gelman diagnostics. However, b_2 did not pass the Heidelberg diagnostics. Also, these results were sensitive to the initial condition: Changing the initial condition to 3 or 4 lynx family groups increased the uncertainty around the b_2 estimate (79% and 63%

probability for a positive b_2; Appendix S1: Table S2). Consequently, from the posterior distribution there is limited support for both a concave (i.e., hump-shaped) and a convex (as indicated by the results) relationship between growth rate and population density.

From the statistical power analysis, the parameter b_2 estimated from the lynx monitoring data was larger and with a positive mean value, compared with a negative mean b_2 from simulated data with a known quadratic density-dependent growth rate (Appendix S2: Figure S6). There was an 89% probability that b_2 from the monitoring data would be larger than the b_2 from the simulated data (Appendix S2: Figure S7).

Model 3—Density-independent growth rate and comparing between southern and central Sweden

The model without density dependence estimated the growth rate ($c_{0-\text{southern}}$) in southern Sweden to be 0.179 (Table 1), which corresponds to a lambda ($\lambda = \exp(c_{0-\text{southern}})$) of 1.197 (±0.031 SD, 95% BCI: 1.137–1.269). The growth rate ($c_{0-\text{central}}$) in central Sweden during the recolonization (1994–2008) was 0.253 (Table 1), which corresponds to a lambda ($\lambda = \exp(c_{0-\text{central}})$) of 1.289 (±0.031 SD, 95% BCI: 1.227–1.354). There was a 97% probability that the growth rate in southern Sweden was lower than in central Sweden. The Bayesian p values were >0.18. The coefficients $c_{0-\text{south}}$ and $c_{0-\text{central}}$ passed both the Heidelberger and Gelman diagnostics.

From the statistical power analysis, the parameter c_0 estimated from the monitoring data was very similar to the estimate from the simulated data with density-independent growth rate, the two posterior distributions largely overlapped (Appendix S2: Figure S8), and there was a 49.5% probability that c_0 from the monitoring data would be smaller than c_0 from the simulated data (Appendix S2: Figure S9). Lastly, the population simulation of Model 3 showed the strongest correlation with the monitoring data compared with simulations from the other two models (Appendix S2: Figure S10).

Model 4—Density-independent growth rate including lynx killed in vehicle collisions comparing between southern and central Sweden

Including lynx killed in vehicle collisions did not change the difference in growth rate between central Sweden and southern Sweden (Table 1). The mean lambda ($\lambda = \exp(d_{0-\text{south}})$) for southern Sweden was 1.229 (±0.029 SD, 95% BCI: 1.175–1.296) and for central Sweden was 1.308 (±0.030 SD, 95% BCI: 1.251–1.371) when including lynx killed in vehicle collisions. There was a 97% probability that the growth rate in southern Sweden was lower than in central Sweden when lynx killed in vehicle collisions were included. The Bayesian p values were >0.16. The coefficients $d_{0-\text{south}}$ and $d_{0-\text{central}}$ passed both the Heidelberger and Gelman diagnostics.

Model selection

We used leave-one-out cross-validation and estimated MSPE to evaluate the different models. Model 3 had the lowest MSPE (24.21), while Model 1 (33.43) and Model 2 (32.12) had similar MSPE, suggesting that Model 3 (density-independent growth rate) had the greatest predictive ability.

DISCUSSION

In this study, we aimed to assess whether the Allee effect was present during the early stage of population establishment during the natural recolonization of a species' previous range. We also assessed whether this recolonization of southern Sweden by lynx took place at a different rate than the previous recolonization of central Sweden. We found that the colonization of southern Sweden occurred more slowly than that of central Sweden, which raised the question as to whether this was due to an Allee effect (i.e., inverse or positive density dependence) in the south. Although only two reproductions were observed at the outset of the natural recolonization of southern Sweden, we did not detect any Allee effect while the population was initially establishing in this area (2004–2021). During this time period, the population increased from approximately 10 lynx (based on two family groups) to about 300 lynx (based on 48 family groups) (Figure 2). Considering that lynx colonized southern Sweden more slowly than central Sweden, it may be expected that there would be an Allee effect (i.e., inverse or positive density dependence) at low population levels, which we did not detect.

The population simulations indicate that there might be some difficulties to detect an Allee effect with an 18-year-long time series. There was a substantial overlap in the probability distributions for the coefficient describing the per capita increase in growth rate (a_1) in the Allee effect model (Model 1) between the monitoring and simulated data (Appendix S2: Figures S4 and S5). The similarity between the results from the monitoring data and the simulated data with a negative quadratic growth rate (Model 2) was weaker (Appendix S2: compare Figures S5 and S7). However, the estimates for the parameter describing density-independent growth rate (c_0) were most similar between the monitoring and simulated data (Appendix S2: Figures S8 and S9) and simulations from the density-independent growth rate model (Model 3) were very similar to the monitoring data (Appendix S2: Figure S10). Furthermore, the model evaluation (leave-one-out cross-validation) suggested that Model 3 (density-independent growth rate) had the greatest predictive ability. Therefore, we conclude that the density-independent growth rate model best described the lynx population development in southern Sweden, but we cannot completely rule out an Allee effect, as some of the simulated population development (about 30%) with a known Allee effect was similar to observed population development. The simulation is based on only one quantitative positive density-dependent growth rate ($a_0 = 0.12$ and $a_1 = 0.00095$, Allee effect; Appendix S2: Table S1, Figure S2). In this alternative, the growth rate at zero density (a_0) was positive. With a stronger Allee effect, for example, with a negative growth at very low densities ($a_0 < 0$), the difference between our monitoring data and simulated data had been larger. On the contrary, with a weaker Allee effect (a_0 larger than the chosen 0.12 and a_1 smaller than the chosen 0.00095), the difference between our monitoring data and simulated data had been smaller. A longer time series will of course increase statistical power to separate between an Allee effect (Model 1 or 2) and density-independent growth rate (Model 3).

There are several models for describing an Allee effect; for example, Courchamp et al. (2008, tab. 3.1) described 14 different models. Several of these models have one feature in common; they describe a concave or hump-shaped relationship between growth rate and population density, and assume a threshold for population density below which the growth rate is negative, known as the Allee threshold. Courchamp et al. (2008) suggested that our Model 2 (quadratic density-dependent growth rate) and our Model 1 (if b_2 in Model 2 is not significantly different from zero) are the most straightforward ways to test for the presence of an Allee effect using long-term monitoring data. Our Models 1 and 2 are very flexible, as they can describe both negative (i.e., include an Allee threshold; a_0 or $b_0 < 0$) and small positive growth rate (a_0 or $b_0 > 0$) at low population densities (Appendix S2: Figure S2).

A low mate encounter rate due to a shortage of mates at low population density is a commonly cited factor explaining an Allee effect (Deredec & Courchamp, 2007). Molnar et al. (2014) showed using process-based modeling that reduced mate finding at low population density can cause an Allee effect in another nonsocial predator, the polar bear. Early in the recolonization period with very low population density, it would be reasonable to expect that a low mate encounter rate could cause a lower growth rate. However, there are reasons to expect that female lynx do not necessarily experience a lack of mating partners when they colonize a new area. Lynx dispersal is male-biased, where most females (ca. 55%) but very few males settle in areas neighboring (within 30 km) their natal home range, and thus, males disperse further (mean 149 km, 32–428 km) than females (mean 46 km, 3–215 km; Samelius et al., 2012). It is thus likely that there is a male-biased sex ratio at the frontier of recolonization. Males also roam over larger home ranges, especially at low population density (Aronsson et al., 2016), increasing the likelihood that females will find a partner despite low density. Therefore, it is likely that the expansion of lynx is limited by female dispersal, which has been shown for other wide-ranging mammals with male-biased dispersal, for example, brown bears (*Ursus arctos*) (Jerina & Adamič, 2008; Swenson et al., 1998) and cougars (*Puma concolor*) (LaRue et al., 2012), rather than female access to mates. That this could have been the case in southern Sweden is supported by spontaneous observations of lynx prior to the first documented reproduction in 2003. In the official carnivore database (Rovbase), 179 observations of lynx were recorded between 1995 and 2002 in southern Sweden. Moreover, lynx have a polygynous mating system in which one male can mate with several females (Aronsson et al., 2016). This would suggest that females do not experience any difficulty in encountering mates during colonization even when population density is low and thus explaining why we did not detect any Allee effect.

Although we could not detect any Allee effect (i.e., inverse or positive density dependence) on the population growth rate, the growth rate during the recolonization of southern Sweden was lower than that during the recolonization of central Sweden (97% probability that the growth rate was lower). One explanation could be that the density of roads and traffic intensity are higher in southern Sweden than in central Sweden, and roads have been shown to be significant causes of mortality or barriers to lynx recolonization elsewhere in Europe (Basille et al., 2013; Schmidt-Posthaus et al., 2002; Zimmermann et al., 2007). Thus, the risk of mortality due to vehicle collisions could be higher in southern Sweden. However, reported traffic-killed lynx did not explain the difference in growth rate when included in our modeling (Table 1). This could be due to that road density and traffic intensity are still relatively low in southern Sweden compared with other parts of Europe, and therefore had less effect on lynx survival.

The lower growth rate could be explained by higher poaching. Andrén et al. (2006) found that poaching accounted for 46% of all adult mortality in Sweden, but with substantial regional variation driven by human–predator conflicts. Heurich et al. (2018) also suggested that increased poaching outside protected areas in central Europe lowered the growth rate and therefore slowed down the expansion of lynx. However, data from radiomarked lynx from southern and central Sweden showed no significant difference in poaching rate (p value $= 0.33$) between the two areas (Andrén, Aronsson, et al., 2022, but specific analyses done in this paper); 1 of 37 radiomarked lynx that were followed for 46 radioyears was assumed to be poached in southern Sweden, resulting in a mean poaching risk of 0.024 (0.00–0.071; 95% CI, Kaplan–Meier estimate). In central Sweden, 7 of 60 radiomarked lynx that were followed for 114 radioyears were confirmed or assumed to be poached lynx, resulting in a mean poaching rate of 0.060 (0.016–0.102; 95% CI, Kaplan-Meier estimate). Another potential explanation for the lower growth rate in southern Sweden could be lower reproduction. However, López-Bao et al. (2019) could not detect any spatial trend in the probability of reproduction, litter size, and kitten survival during the first 9 months from southern to central Sweden. One more explanation could be that source areas were not saturated and therefore provided relatively few female immigrants. Female lynx disperse shorter distances than males, and most young females settle very close to their natal area if possible (Samelius et al., 2012). Furthermore, the lynx population in Sweden is managed through licensed hunting, whereby adult individuals are removed from the population regularly, potentially creating a continuous availability of vacant areas for lynx settled in central Sweden. As a result, there was presumably an abundance of vacant areas suitable for lynx settlement in central Sweden, which may have limited the rate of dispersal of females to southern Sweden. Fewer emigrants from central Sweden likely result in lower connectivity with southern Sweden, which in turn result in a lower growth rate.

In addition to the potential influence of short female dispersal distance on recolonization, central Sweden and southern Sweden are separated by three large lakes, a network of highways, and large areas of agricultural landscape (Hemmingmoore et al., 2020). These areas of less suitable lynx habitat disrupt the mainly continuous distribution of high habitat suitability in central and southern Sweden. Lynx are able to cross these barriers, allowing colonization of southern Sweden. However, no such barrier exists between central Sweden and northern areas from which lynx originally recolonized (Samelius et al., 2012). The difficulty encountered by lynx crossing unsuitable habitat could be discouraging and thus slow down recolonization, as seen in other European populations (Magg et al., 2016; Niedziałkowska et al., 2006).

The ability to understand and assess the viability of small and recovering populations is very important in conservation and management. That an Allee effect was absent or unlikely to have occurred during the recolonization of lynx in southern Sweden is, despite a lower population growth rate, positive for conservation of this and other systems. Although this study was based on an 18-year-long series, more data would likely strengthen the conclusion. Some populations of large carnivores in North America (Smith et al., 2016) and Europe (Chapron et al., 2014) are recolonizing their former ranges, which can begin with a small population at the frontier of recolonization. If these species were to face an Allee effect in addition to other barriers to recovery, it would have a negative effect on the viability of small populations, as the growth rate would be even lower at low population sizes (Courchamp et al., 1999). The loss of continuous habitat is one of the most significant factors in contributing to lost resiliency and megafauna population decline worldwide (Courchamp et al., 2008; Tucker et al., 2018; Woodroffe, 2006). In Sweden, the potential barriers for lynx did not prevent recolonization of southern Sweden, although the lower growth rate illustrates the effect that even permeable barriers may have on the carnivore recovery.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Henrik Andrén conceived the idea and designed the study, which was further developed in discussions with all the other coauthors. Henrik Andrén and Heather Hemmingmoore prepared the database. Henrik Andrén did most of the analyses with input from Malin Aronsson and Heather Hemmingmoore. Henrik Andrén wrote the first version of the manuscript with input from the other coauthors. All authors contributed to the writing of the manuscript and approved the final version for publication.

DATA AVAILABILITY STATEMENT

Data and statistical R codes for the Bayesian hierarchical population models (Andrén, Hemmingmoore, et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.8kprr4xqb.

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SUPPORTING INFORMATION

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