



Life-cycle analysis of an endangered migratory goose to assess the impact of conservation actions on population recovery

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ABSTRACT

Evaluating the effectiveness of conservation actions is challenging for migratory species because a population can be impacted anywhere along its route. Conservation actions for the critically endangered Fennoscandian lesser white-fronted goose population include culling of red foxes in the breeding area and habitat improvements and reduction of illegal hunting in the non-breeding areas. One goal of the predator control strategy is to prevent adult birds from using an autumn migration route through western Asia, where mortality is believed to be higher than on the migration route through eastern Europe. We used 23 years of count data obtained at different staging areas to parameterize a seasonal state-space model describing the full-annual cycle dynamics of this population and evaluate whether the recent population recovery was linked to these conservation efforts. The results did not provide evidence that predator control influenced population recovery, as survival on the European route did not appear higher than on the allegedly riskier Asian route. However, adult survival at staging areas on both routes and at wintering sites may have improved in the last decade, suggesting a positive effect of the other conservation initiatives. These results emphasize the importance of including the non-breeding dynamics in population assessments of migratory species and highlight the challenge of evaluating the efficacy of separate conservation actions when a proper experimental design is unfeasible. Our study, which is a unique case of cross-national, coordinated conservation efforts, exemplifies how to model complex population dynamics to assess the influence of costly conservation initiatives.

1. Introduction

Information on demographic processes such as survival, fecundity and recruitment is crucial to develop effective population management strategies (Mills, 2007; Williams et al., 2002). When such information is lacking, we risk to direct management efforts at processes that have little impact on population growth rate (Johnson et al., 2010). When managing bird populations, for instance, focusing on improving nesting success is common even though the contribution of the latter to population dynamics is often unknown (Gaines et al., 2020). For small and endangered populations, we typically lack detailed demographic data,

forcing us to rely on knowledge obtained from other populations or different species to identify management actions. This may be hazardous because the relative importance of demographic processes can differ greatly between healthy and declining populations of the same species, let alone of different species (Beissinger and Westphal, 1998; Johnson et al., 2010).

Understanding the demographic processes underlying population dynamics is even more challenging for migratory species, because factors that limit population growth can operate at different locations throughout the annual cycle (Sutherland, 1996). Environmental conditions experienced at each location may have both direct (i.e.,

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immediate) and carry-over (i.e., delayed) effects on population dynamics, adding another layer of complexity (e.g. Layton-Matthews et al., 2020; Rockwell et al., 2012). In the case of migratory birds, studies often focus on the breeding season only. However, over the course of a year, birds usually spend more time at non-breeding sites (Faaborg et al., 2010) and limitations during the non-breeding period may be the primary drivers of population dynamics (Rushing et al., 2017; Wilson et al., 2018). Thus, more investigations assessing population dynamics throughout all stages of the annual cycle are needed (Hostetler et al., 2015; Marra et al., 2015; Rushing et al., 2016).

The lesser white-fronted goose *Anser erythropus* is a migrant goose species that breeds in sub- and low-arctic tundra and overwinters in temperate wetlands across Eurasia. Once common in northern Fennoscandia, the Fennoscandian population experienced a drastic decline during the 20th century, reaching its minimum size in 2008 at less than 15 remaining breeding pairs (Aarvak et al., 2009). A large conservation network spanning several countries across the population's range was established already in the mid-1980s, with the aim of improving knowledge and conservation of this population (Ekker and Bø, 2017). Efforts to control predators (culling of red fox *Vulpes vulpes*) in the core breeding area in northern Norway during 2008–2020 were believed to be one of the main reasons for the recent recovery of the population (Aarvak et al., 2017). Predator control was started with two goals: increasing reproductive success and reducing early reproductive failure. The latter was considered crucial, because early-failing breeders seem to leave the breeding areas earlier in the reproductive season than late-failing and successful breeders, and to subsequently embark on a longer migratory journey through western Asia (here termed “Asian route”). Survival is expected to be lower on the Asian route than on the migration route through eastern Europe (here termed “European route”) due to higher hunting pressure (Øien et al., 2009; Fig. 1). By reducing early reproductive failure, adult birds would start moulting close to the breeding sites, becoming flightless for several weeks and unable to take the Asian route. Since 2008, an estimated 22–43 % of the local red fox

population has been culled every year between February and May, before the arrival of the geese at their breeding site (Marolla et al., 2019). Marolla et al. (2019) did not find evidence that this predator control actually improved goose breeding success, which instead appears to be driven primarily by the functional response of the predator guild to cyclic dynamics of small rodent populations (Marolla et al., 2019). However, the goose population increased significantly within the predator control period, perhaps due to subtle indirect demographic effects of this management action. Still, it remains unclear whether the influence of predator control on the choice of the autumn migration route could have influenced adult survival and contributed to the population recovery (Marolla et al., 2019).

Here, we modelled the population dynamics of the Fennoscandian population of lesser white-fronted goose at different stopover sites along its migration routes using 23 years (1998–2020) of count data. Our primary goal was the estimation of seasonal vital rates and the comparison of survival probabilities between the two migration routes. We were also interested in assessing the effects of predator control at the breeding site and comparing these effects to the potential effects of other conservation initiatives carried out at one of the staging areas in Hungary and in the wintering areas in Greece. These conservation initiatives aimed at minimizing illegal shooting and improving habitat quality (Vougioukalou et al., 2017). We expected 1) survival on the allegedly riskier Asian migration route to be lower than on the European route; 2) a decrease in the probability of birds taking the Asian route after the start of predator control in 2008; 3) the change in this probability to be of larger magnitude than changes in other vital rates; and 4) survival to increase after the implementation of conservation actions in the staging and wintering areas.

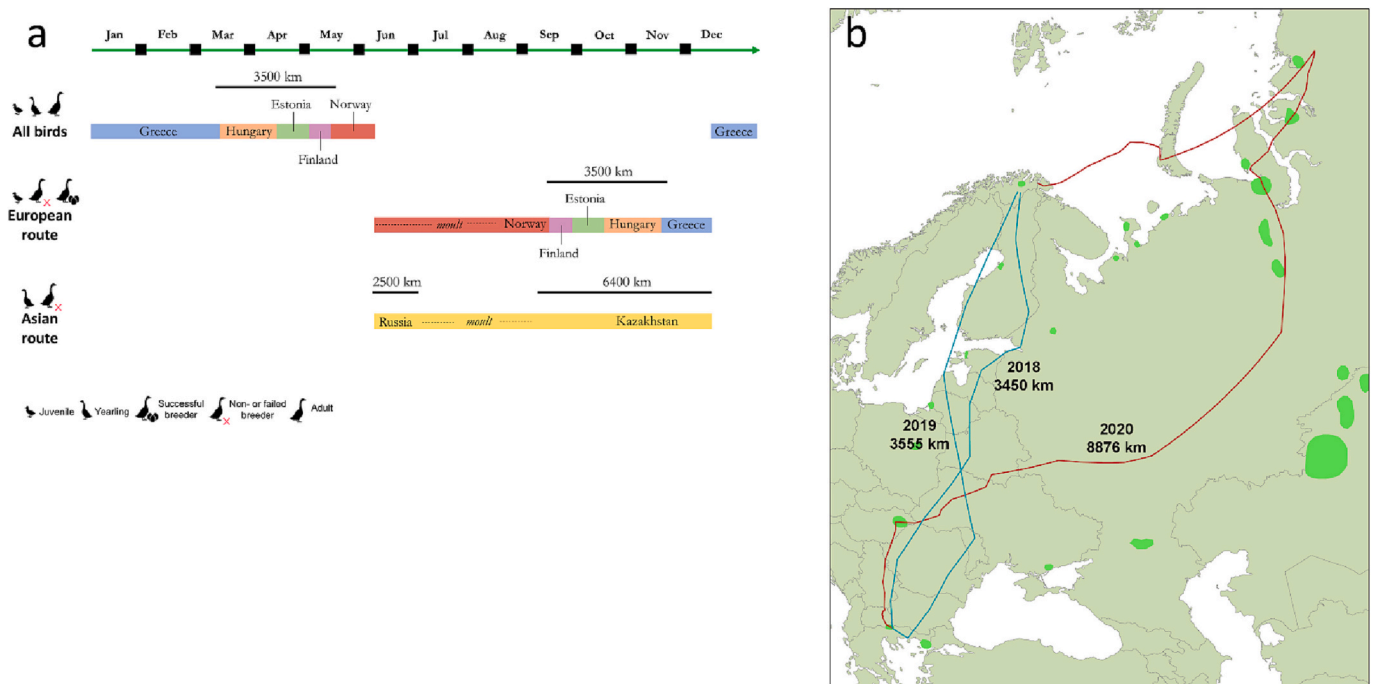


Fig. 1. (a) Schematic representation of the migratory cycle of the Fennoscandian lesser white-fronted goose population. (b) Autumn migration of an adult male of lesser white-fronted goose caught by BirdLife Norway at the Valdak Marshes in May 2018 and equipped with a GPS-GMS neckband that collects a GPS-location every sixth hour (map from Øien and Aarvak, 2021). The male, later known as Mr. Blue, flew the European route in 2018 and 2019 – after rearing three and two goslings respectively – and the Asian route in 2020 – after breeding failure. Brighter green areas indicate major staging, wintering and moulting sites for both the Fennoscandian and the west Russian population. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Migration routes

The Fennoscandian population of lesser white-fronted goose performs a seasonal migration between wintering grounds in Greece and breeding areas in Finnmark County, northern Norway (Fig. 1a). The reproductive season lasts from late May to mid-August. Adult birds leave the breeding areas with fledglings in September, after a staging period of about three weeks in the inner parts of Porsangerfjord, Norway (70°10'N 24°40'E). The European route takes them via Finland and/or north-western Russia. From there, the birds may choose different paths southward through Eastern Europe, where they often have an important stopover at Hortobágy National Park in eastern Hungary, to finally reach the wintering areas at Lake Kerkini and in the Evros Delta in northern Greece (Øien and Aarvak, 2021). Spring migration starts in March and follows approximately the same route, simply in the opposite direction, but with regularly used staging sites on the coasts of Estonia and Bothnian Bay in Finland. Birds return to the staging areas at Valda Marshes in mid-May and move to the core inland breeding area (~50 km away) about a week later (Aarvak and Øien, 2003). Field observations combined with a few color ring resightings and satellite telemetry data suggest that birds that do not breed or fail in their breeding attempt early in the season may undertake an eastward and subsequently southward migration to reach the wintering grounds in Greece through western Russia, north-central Siberia, and north-western Kazakhstan – the Asian route (Aarvak and Øien, 2003; Øien et al., 2009; Aarvak and Øien, 2023; Fig. 1b). Birds on the Asian route make an important stopover at large moulting areas in western Russia, between the Kanin and the Taymyr peninsulas, where other migratory birds gather to moult (Aarvak and Øien, 2003). The reason behind the moult migration behaviour is unknown, but it might be related to low predation pressure linked to specific geographic areas and predator swamping (Piironen et al., 2021). On the Asian route, the risk for geese to be shot illegally is expected to be higher (Jones et al., 2017). Several recoveries of shot birds in these areas provide anecdotal support for this hypothesis (Marolla et al., 2019). Between 1995 and 2006, seven out of ten failed breeders took the Asian route, of which two were later confirmed to have been shot and three were suspected to have been shot (Aarvak and Øien, 2003; Lorentsen et al., 1999; Øien et al., 2009). This is in addition to four confirmed shot recoveries of ringed lesser white-fronted geese along the Asian route during the same period (Lorentsen et al., 1999). Lower adult survival on this supposedly riskier migration route through western Asia was perceived as a cause of population decline (Øien and Aarvak, 2009). Red fox predation on eggs and chicks of ground-nesting birds, including geese (Kristiansen, 1998), is a cause of early breeding failure. Therefore, one goal of the predator control program was to reduce early breeding failure, and thus restrict the number of birds venturing on the Asian route.

2.2. Population counts

The goose population is monitored at different locations along the European route. We used maximum counts between 1998 and 2020 at three major stopovers in northern Norway, Hungary, and Greece, where the population breeds, stages, and overwinters, respectively. At each location, birds are assigned to age classes whenever possible.

In Norway, counts have been carried out at the staging sites at the Valda Marshes in spring (May–June, since 1990) and autumn (August–September, since 1994), i.e. before and after the breeding period. Double counting of individuals occurs very seldom due to unique patterns in the black belly-patches that allow individual recognition within a season (Øien et al., 1996). Individuals, however, cannot be identified across years because these patterns change between years (Aarvak et al., 2009). In spring, the numbers of yearlings (i.e. 2nd calendar-year birds), breeders (i.e. ≥3rd calendar-year birds that are

part of a breeding pair) and non-breeders (i.e. ≥3rd calendar-year birds that are not part of a breeding pair) were recorded. In autumn, fledglings, successful breeders (i.e. birds in a breeding pair with at least one fledgling), and unsuccessful breeders (i.e. birds not part of a family group) were counted. Information on clutch size and early chick survival was not available because during summer birds spread across the breeding area and are difficult to survey.

In Hungary, counts have been carried out at Hortobágy National Park during both spring and autumn migration since 1990. Long distances between birds and observers as well as frequent presence of heat haze in this hot steppe area did not allow easy differentiation between young and adult birds. Therefore, only the total number of birds observed is available.

In Greece, reports of staging lesser white-fronted geese date back to the early 1900s. Systematic, reliable counts, however, have only been carried out since 2005. Weekly counts were performed at the two major staging areas of Lake Kerkini and in the Evros Delta during the goose winter staging period from as early as October until as late as March. At both sites, conditions allowed for identification of juveniles and adults during autumn and early winter.

2.3. Demographic model

Estimating demographic rates of animal populations typically requires marking and recapturing of individuals. Protocols ensuring individual recognition can be difficult to implement (Rodríguez-Caro et al., 2019) especially for endangered populations (Wielgus et al., 2008). Count data, however, are often available for birds and many other animal taxa (Link and Sauer, 1998). To circumvent the issue of marking animals, various statistical methods for demographic assessment based on count data of unmarked individuals have been developed (e.g. Gross et al., 2002; Gross et al., 2005; Link et al., 2003; Rodríguez-Caro et al., 2019; Zipkin et al., 2014). Methods using age-class-specific counts to estimate vital rates are typically referred to as “inverse modelling” (Caswell, 2000; González et al., 2016). Here, we built a seasonal, stage-structured, state-space population model for the lesser white-fronted goose population based on stage-structured count data. In the state-space modelling framework, an observation process that accommodates the measurement error of the results of a survey, as well as the lack of fit of the process model, is linked to an underlying population dynamics model for the true stage-specific abundance, i.e., the process model (de Valpine and Hastings, 2002; Kéry and Schaub, 2012). Therefore, the true population abundances are modelled as latent state variables, while the observations are modelled as conditional on these unknown states. We used Bayesian methods to fit our model, estimate demographic parameters, evaluate associated uncertainty, and obtain insights into important stage-transitions in the population dynamics of Fennoscandian lesser white-fronted geese.

2.3.1. Model of population dynamics

The life-cycle model of the Fennoscandian lesser white-fronted goose population is shown in Fig. 2. The model included four stopover locations that matched the locations where the population counts were made, i.e., Norway Spring (pre-breeding survey), Norway Autumn (post-breeding survey), Greece Winter, and Hungary Spring. We chose to not include counts from Hungary during the autumn migration because data from the last ten years suggested a change in stopover strategy of birds there. We decided to start the annual cycle in Norway Spring, i.e., the pre-breeding survey at the Valda Marshes staging sites in Norway. We included five stage classes that are a combination of three age classes (juveniles or 1st calendar-year birds; yearlings or 2nd calendar-year birds; adults or ≥3rd calendar-year birds) and three states of reproductive status for the oldest age class (non-breeders, failed breeders, and successful breeders). We assumed an even sex ratio for fledglings and adults, and identical survival for both sexes (Pistorius et al., 2007). We also assumed that breeding begins at age 2, because yearlings have never

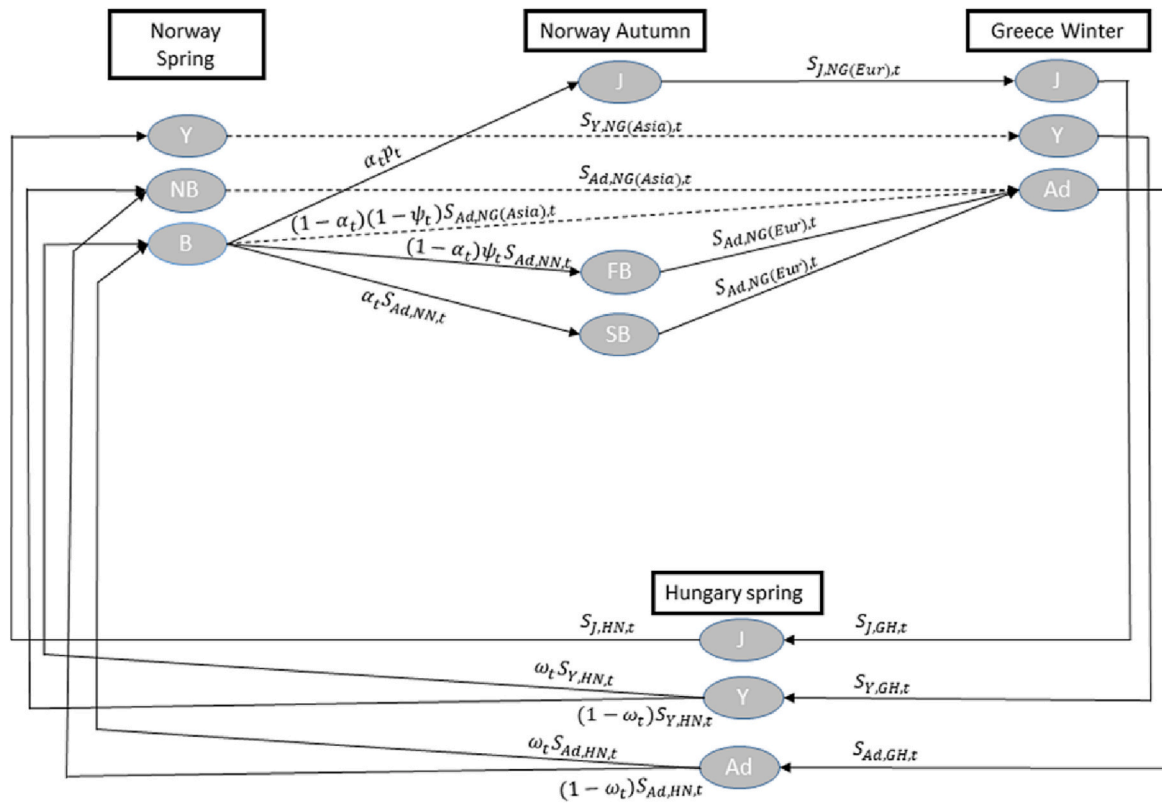


Fig. 2. Life cycle of the Fennoscandian lesser white-fronted goose population. Dashed arrows depict the allegedly riskier migration route through western Asia (the Asian route). Y = Yearling; NB = Non-Breeder; B = Breeder; J = Juvenile; FB = Failed Breeder; SB = Successful Breeder; Ad = Adult. Definitions of demographic parameters can be found in Table 1.

been observed associated with fledglings during post-breeding surveys (Aarvak and Øien, 2009). This is a sensible assumption because goose species typically do not breed before turning 2 years old (Finney and Cooke, 1978; Viallefont et al., 1995; Warren et al., 1992).

The reproductive status and success of adults determine whether an individual will undertake the migration to the wintering grounds in Greece through the European or the Asian route. Successful breeders are assumed to always fly along the European route and non-breeders to always fly along the Asian route, while breeders that failed breeding at an early stage are assumed to choose between the two routes. Yearlings do not breed, so they are assumed to always fly the Asian route. Because we adopted a seasonal model, stage-specific abundances across consecutive stopovers are a function of seasonal survival, fecundity, and stage-specific abundance at the previous stopover. To account for demographic stochasticity in this small population, stage-specific abundances were described as outcomes of stochastic processes. We linked the observed counts to the latent stage-specific abundance through conditional probabilities, assuming no systematic over- or underestimation of counts at any of the four stopover sites. We provide a detailed description of the model and associated assumptions in Appendix S1 and a list of the parameters in the model in Table 1. These include stage-specific survival probabilities for the different migration legs. We acknowledge that these survival probabilities are likely estimates of apparent survival. Indeed, the migratory range of the Fennoscandian lesser white-fronted goose population partially overlaps with that of the neighbouring west Russian population as they share part of the Asian migration route (Øien and Aarvak, 2009), and some immigration of males from the Russian population has been reported (Ruokonen et al., 2010). Because the Fennoscandian population is considered a single management unit (Ruokonen et al., 2004), we also assumed it to be a distinct demographic unit in our study.

2.3.2. Population growth rate

Based on model estimates of annual population size, we calculated the annual population growth rate λ_t by dividing the total population size in Norway Spring in year $t + 1$ by the total population size in Norway Spring in year t :

$$\lambda_t = (N_{Y,NS,t+1} + N_{B,NS,t+1} + N_{NB,NS,t+1}) / (N_{Y,NS,t} + N_{B,NS,t} + N_{NB,NS,t})$$

where $N_{Y,NS}$ is the number of yearlings in Norway Spring, $N_{B,NS}$ is the number of breeders in Norway Spring, and $N_{NB,NS}$ is the number of non-breeders in Norway Spring.

2.3.3. Demographic assessment of goose management

When we tried to estimate the temporal variability in all vital rates in our fairly complex model, issues of parameter identifiability arose with our data set. With the available count data, we could not estimate probabilities of seasonal survival and of choosing the Asian route that vary annually. To assess the effects of the predator control program on the probability that failed breeders avoid the allegedly riskier migration route (ψ_t), we tested whether ψ_t changed after the implementation of the culling program in 2008 by modelling it as a function of a categorical variable *management*, which indicates whether fox culling occurred in a given year (*management* = 1) or not (*management* = 0). We used a logit link function to model this probability:

$$\text{logit}(\psi_t) = \mu_\psi + \beta_{\text{management},\psi} \times \text{management}_t$$

where μ_ψ is the logit of the probability in years prior to the management action. By looking at the effect of *management* on ψ_t , we assessed the potential of fox culling to reduce early breeding failure. If breeding failure is delayed, an adult bird would start moulting in the breeding area and remain in Norway throughout the summer, thus avoiding the Asian route.

Table 1

Definition of parameters in the Fennoscandian lesser white-fronted goose population model, along with estimated posterior means and 95 % credible intervals for the whole study period (1998–2020).

Parameter	Definition	Posterior mean	95 % CRI
α	Probability of breeding successfully	0.33	0.23; 0.43
p	Product of fecundity and chick survival	0.50	0.29; 0.80
ψ	Probability that a failed breeder chooses the European route	0.30	0.07; 0.58
ω	Probability of becoming part of a breeding pair	0.90	0.86; 0.94
$S_{Ad,NN}$	Adult survival from Norway Spring to Norway Autumn	0.93	0.83; 1.00
$S_{Ad,NG (Eur)}$	Adult survival from Norway Autumn to Greece Winter via Europe	0.90	0.65; 1.00
$S_{Ad,GH}$	Adult survival from Greece Winter to Hungary Spring	0.92	0.80; 1.00
$S_{Ad,HN}$	Adult survival from Hungary Spring to Norway Spring	0.98	0.94; 1.00
$S_{Ad,NG (Asia)}$	Adult survival from Norway Spring to Greece Winter via Asia	0.91	0.70; 1.00
$S_{J,NG (Eur)}$	Juvenile survival from Norway Autumn to Greece Winter via Europe	0.70	0.53; 0.88
$S_{J,GH}$	Juvenile survival from Greece Winter to Hungary Spring	0.87	0.67; 0.99
$S_{J,HN}$	Juvenile survival from Hungary Spring to Norway Spring	0.83	0.63; 0.99
$S_{Y,NG}$	Yearling survival from Norway Spring to Greece Winter	0.82	0.49; 0.99
$S_{Y,GH}$	Yearling survival from Greece Winter to Hungary Spring	0.88	0.62; 1.00
$S_{Y,HN}$	Yearling survival from Hungary Spring to Norway Spring	0.89	0.63; 1.00
β_{rodens}	Effect of small rodent abundance on p	0.06	0.04; 0.07

Conservation initiatives other than the predator control program, however, were launched around 2005 and then implemented throughout 2010s at the autumn staging site in Hungary and at the wintering sites in Greece. These initiatives aimed at minimizing poaching and accidental shooting as well as improving habitat quality and could have contributed to the population increase. Therefore, we also assessed whether adult autumn survival probabilities on the European route ($S_{Ad,NG(Eur),t}$) and adult winter survival ($S_{Ad,GH,t}$) were different before and after 2008. For consistency, we also tested for a change after 2008 in adult survival on the Asian route ($S_{Ad,NG(Asia),t}$). These three survival probabilities were modelled with a customary logit function:

$$\text{logit}(S_{Ad,NG(Eur),t}) = \mu_{S_{Ad,NG(Eur),t}} + \beta_{\text{management},S1} \times \text{management}_t$$

$$\text{logit}(S_{Ad,GH,t}) = \mu_{S_{Ad,GH,t}} + \beta_{\text{management},S2} \times \text{management}_t$$

$$\text{logit}(S_{Ad,NG(Asia),t}) = \mu_{S_{Ad(Asia),NG,t}} + \beta_{\text{management},S3} \times \text{management}_t$$

where μ_{S_x} is the logit of the probability in years prior to the management action. Also, because only the maximum number of birds observed throughout the complete wintering period in Greece was available for this study, the parameter that we call ‘adult winter survival’ ($S_{Ad,GH,t}$) overlaps and thus is partly confounded with survival during autumn migration between Norway and Greece.

2.3.4. Model fitting

We fitted the model in R using Markov chain Monte Carlo methods implemented in JAGS (Plummer, 2003) via the R package jagsUI (Kellner, 2015). We assigned vague priors to all parameters and slightly more constrained priors to the $\beta_{\text{management},\psi}$ and $\beta_{\text{management},Sx}$ parameters

to improve rates of convergence (i.e. normal distributions with mean = 0 and variance = 10). To initiate the model, we provided initial population abundances in Norway Spring at $t = 1$ (i.e. $N_{Y,NS,1}$, $N_{NB,NS,1}$ and $N_{B,NS,1}$) using available data. We ran four chains with 500,000 iterations each, of which 100,000 were discarded as a burn-in and every 50th sample kept of the remainder, yielding 32,000 draws from the joint posterior distribution of the parameters. Convergence of Markov chains was evaluated by visual inspections of trace plots of the draws and by ensuring that the Gelman-Rubin convergence statistics R-hat were all below 1.1 (Brooks and Gelman, 1998). We summarised posterior distributions by their mean and 95 % credible interval [CRI].

3. Results

Our model estimated that the Fennoscandian population of lesser white-fronted goose declined from 68 [95 % CRI: 59; 77] birds in Norway Spring in 1998 to 39 [32; 46] birds in Norway Spring in 2007, the year before the start of the predator control program. The population reached its lowest level in 2009 with 35 estimated birds [29; 42], and then increased up to 112 birds [102; 122] in 2017. Eventually, it experienced a new, small decrease and reached 97 [87; 108] individuals in 2020 (Fig. 3). Notably, the population did not increase gradually after 2009, but rather experienced two abrupt positive changes in abundance after summers with high abundances of small rodents in 2011 and 2015 (Fig. S1; see Appendix S1 for a description of small rodent data). Annual population growth rate λ_t changed from an average of 0.95 [0.77; 1.17] before the onset of the predator control program to 1.10 [0.93; 1.29] afterwards.

Estimates of all demographic parameters are shown in Figs. 4 and 5 and Table 1. Average juvenile apparent survival along the European route ranged between 0.70 [0.53; 0.88] and 0.87 [0.67; 0.99] depending on the migration leg, while average yearling apparent survival along the Asian route ranged between 0.82 [0.49; 0.99] and 0.89 [0.63; 1.00], and average adult apparent survival ranged between 0.90 [0.65; 1.00] and 0.98 [0.94; 1.00]. Importantly, and contrary to our expectations, average adult apparent survival on the supposedly riskier Asian route (0.91 [0.70; 1.00]) was estimated to be of very similar magnitude as the one estimated for the European route (0.90 [0.65; 1.00]), although a large uncertainty precludes drawing firm conclusions. By taking the product of average apparent survivals for all migratory legs, we also estimated annual survival for adults that flew the European route (0.75 [0.56; 0.89]) or the Asian route (0.82 [0.65; 0.93]), as well as for juveniles (0.49 [0.38; 0.60]) and yearlings (0.65 [0.32; 0.87]).

With respect to the effects of the management actions evaluated in our model, the average probability for failed breeders to avoid the Asian route (ψ) did increase from 0.31 [0.08; 0.59] to 0.71 [0.51; 0.96] after the implementation of the predator control program ($\beta_{\text{management},\psi} = 1.91$ [0.42; 4.23]; Fig. 6). Apparent adult survival probabilities were also estimated higher on average after the onset of predator control, but estimates of change had high uncertainty (Fig. 6): European route survival increased by 10.3 [−3.9; 48.9]% ($\beta_{\text{management},S1} = 2.49$ [−1.43; 7.23]), wintering survival by 8.74 [−0.2; 25.1]% ($\beta_{\text{management},S2} = 3.29$ [−0.19; 7.62]) and Asian route survival by 7.04 [−13.6; 37.5]% ($\beta_{\text{management},S3} = 1.95$ [−2.07; 6.92]).

4. Discussion

We took advantage of 23 years of population surveys producing count data at several stages across the entire annual range of the migratory Fennoscandian population of lesser white-fronted goose to parameterize a seasonal, stage-classified, state-space model and address several unanswered and hotly debated questions about the contributions of multiple conservation actions to the recent population recovery. Such evaluations are crucial when a proper experimental design including controls and spatial and temporal replications is unfeasible, which is

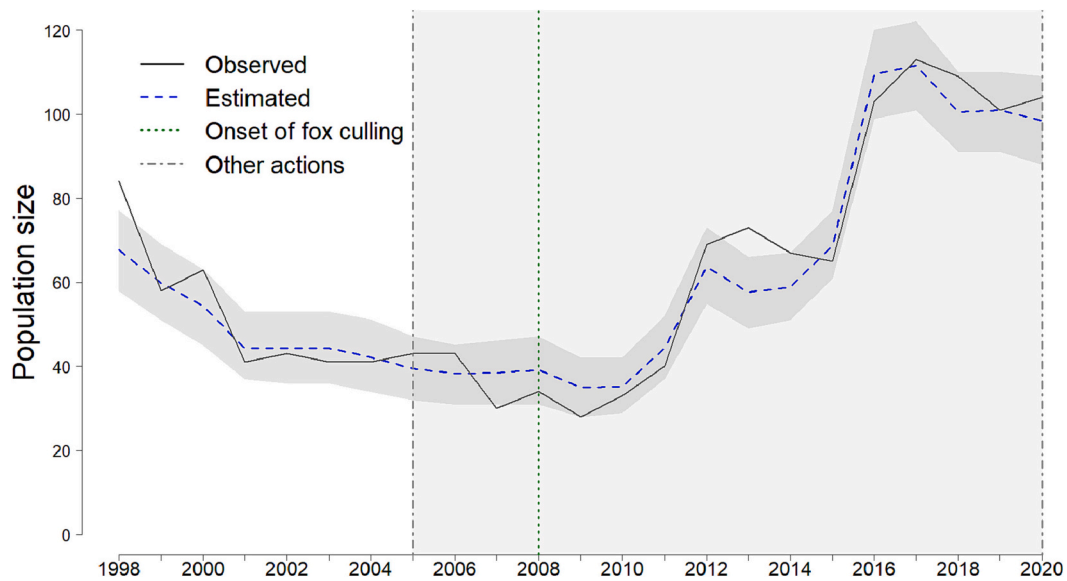


Fig. 3. Observed and estimated total number of individuals of the Fennoscandian lesser white-fronted goose population in Norway Spring. The dark gray area around the lines represents 95 % credible intervals. The vertical dashed green line represents the initiation of the red fox culling program. The large light-gray area, delimited by the vertical dotted gray lines, represents the period when conservation actions other than the predator control program were implemented in countries that host key staging sites for the goose population. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

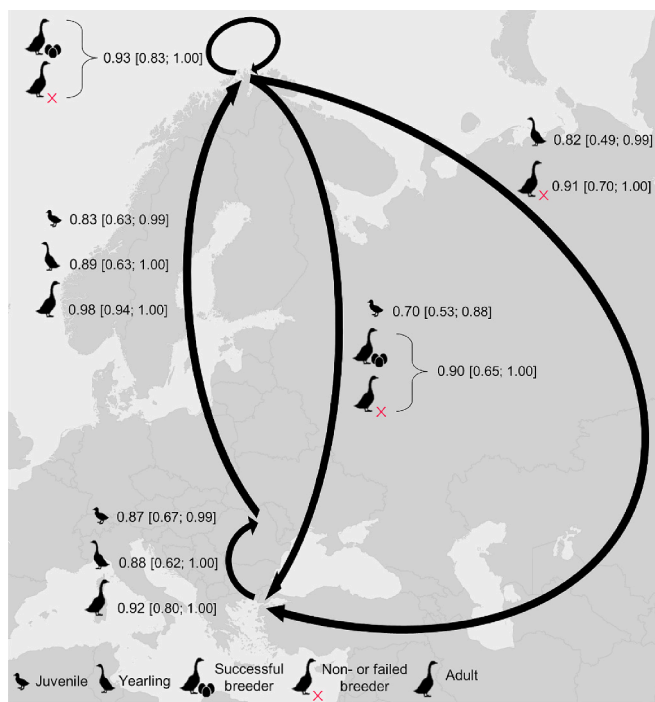


Fig. 4. Simplified representation of the life cycle of the Fennoscandian lesser white-fronted goose population with the two migration routes, i.e. the European route and the Asian route. Numbers are estimates (posterior mean \pm 95 % Credible Interval) of stage class and leg-specific survival probabilities. For graphical purposes, the arrows show an approximation of the itinerary covered by the birds.

typical of endangered species that are far too small for an experimental approach to be pursued. Our study assessed population dynamics accounting for the non-breeding period, an aspect often ignored in many studies on migratory species, and our results highlighted that this period seems to be at least as critical as the breeding period. Our study also highlights that the influence of the predator control program, which was

believed to be a main driver of population recovery, is in fact supported by poor evidence. This result emphasizes the fundamental necessity to assess conservation actions after their implementation, an aspect that is often neglected in too many conservation initiatives. Our study is thus a unique case of cross-national, coordinated conservation efforts, providing an example on how to model complex population dynamics in species with sparse data and complex behaviour, allowing to assess the influence of costly conservation initiatives.

Because a previous study was unable to demonstrate any evidence for an effect of predator control on reproductive success (Marolla et al., 2019), this study focused on the possibility that predator control could have influenced the goose population growth rate via its effect on the birds' migratory behaviour and the survival probabilities associated with the different migration routes. Indeed, predator control in the breeding area in northern Norway was initiated not only to increase reproductive success, but also to reduce early breeding failure, which is believed to induce birds to migrate through western Asia instead of eastern Europe. Illegal hunting, and thus mortality, was expected to be higher on the Asian migration route than along the European route (Aarvak and Øien, 2003; Jones et al., 2017; Lorentsen et al., 1999; Øien et al., 2009).

Contrary to expectation, the estimated adult survival on the Asian route was, on average, similar to that on the European route. This suggests that birds had similar mortality risk on both routes. Still, survival on both routes tended to increase after culling of red foxes was implemented. Furthermore, despite some statistical uncertainty, the average probability that failed breeders avoided migrating through Asia more than doubled after the initiation of fox culling (Fig. 6). We may infer that the predator control program achieved its purpose of increasing the proportion of geese migrating on the European route. This effect, however, may not have had a considerable influence on the population growth rate because the Asian route appeared not to be as risky as expected. Still, the large uncertainty associated with the survival estimates may have masked any small differences in mortality risks that may have existed between the two migration routes. Moreover, potential immigration of geese from the Russian population during the autumn migration through western Asia may have confounded the estimates of survival to a currently unknowable degree. However, all in all, based on our model, data, and findings of Marolla et al. (2019), we are unable to demonstrate that predator control, as conducted so far, has influenced

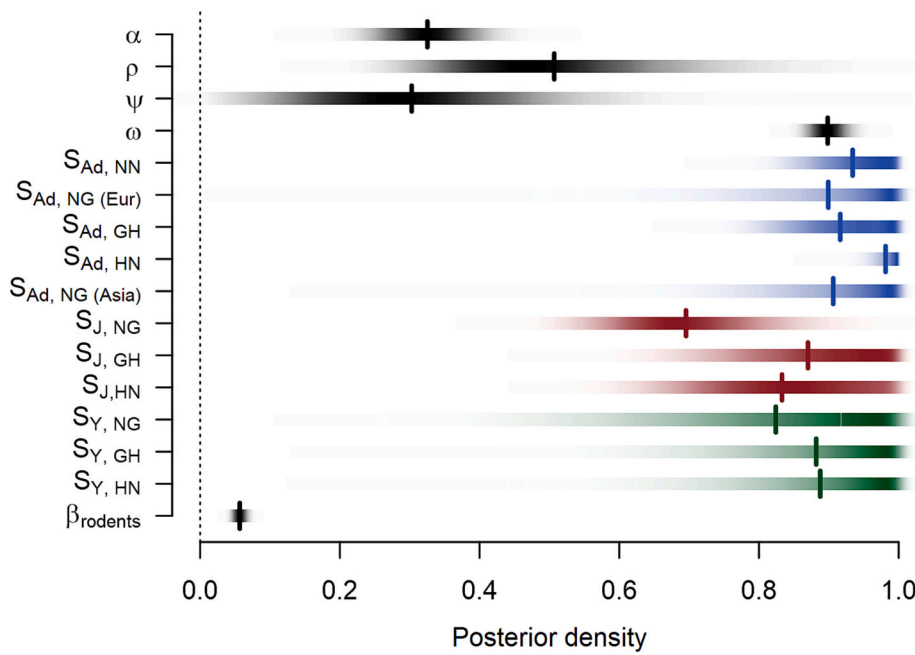


Fig. 5. Posterior densities of vital rates in the Fennoscandian lesser white-fronted goose population model (darker means higher density). Vertical lines show posterior means. All parameters except $\beta_{rodents}$ and p are probabilities and thus vary between 0 and 1. Survival probabilities are grouped by stage class and reported following the goose migration scheme (from top to bottom). Survival parameters referring to the same age class have identical colors. For interpretation of the labels, see Table 1.

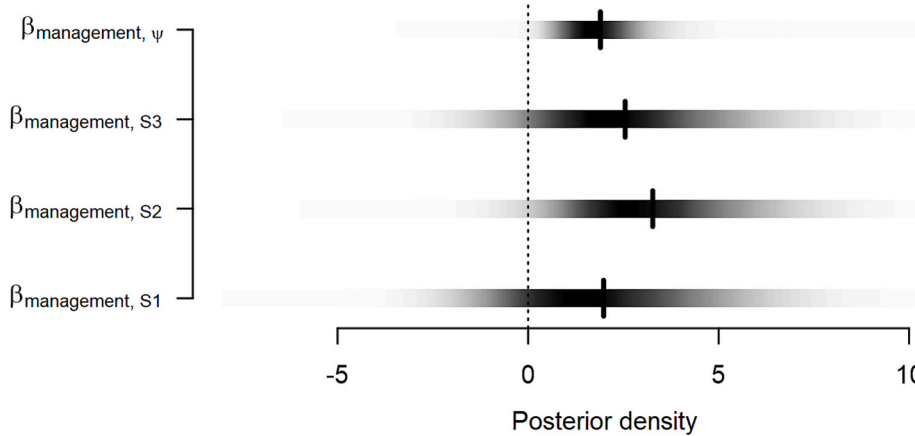


Fig. 6. Posterior densities of estimated changes (on logit scale) in the four selected vital rates after the implementation of the predator control program in 2008 (darker means a higher density). Vertical lines show posterior means. $\beta_{management.S1}$ = change in adult survival from Norway Autumn to Greece Winter (i.e., autumn migration on the European route plus a portion of winter staging). $\beta_{management.S2}$ = change in adult survival from Greece Winter to Hungary Spring (i.e., a portion of winter staging plus the first leg of spring migration on the European route). $\beta_{management.S3}$ = change in adult survival from Norway Autumn to Greece Winter on the Asian route. $\beta_{management,\psi}$ = change in the probability that failed breeders avoid the Asian route.

the growth rate of this lesser white-fronted goose population. Interestingly, our analysis suggested that the probability of avoiding the Asian route might not be the only parameter that changed in the years following the onset of predator control. After 2008, average survival probabilities on both migration routes and wintering grounds increased, but the large estimation uncertainty precludes any strong conclusions about the magnitude of these changes. Nonetheless, this result may reflect a positive effect of the set of conservation interventions that were implemented to improve bird safety at several staging areas along the European route. Between 2005 and 2020, many of the countries that host the Fennoscandian lesser white-fronted goose population during parts of its annual cycle started an international cooperation supported by two EU LIFE-Nature projects (Vougioukalou et al., 2017). In several of the countries involved, these initiatives led to the development of National Action Plans for the lesser white-fronted goose. Patrolling systems were implemented in Greece and Bulgaria to prevent poaching and accidental shooting, habitats were restored at the main staging site in Hungary and at wintering sites in Greece, public awareness campaigns were launched, and conservation actions were recommended also in the countries located along the Asian route (Vougioukalou et al., 2017). Moreover, in Greece, hunting of all goose

species was banned in special protected areas including the Evros Delta in 2012 (Vougioukalou et al., 2017). A shift in wintering sites from the Evros Delta to Lake Kerkini might also have reduced accidental shooting. Remarkably, no lesser white-fronted geese were found shot at project sites in Greece during the second LIFE project (2011–2017; Vougioukalou et al., 2017), but then the economic crisis in 2008 may have contributed to a decrease in hunting activities in Greece (Kazantzidis et al., 2015). In addition, along the autumn migration corridor in Kalmykia, Russia, a moving, temporary nature reserve with hunting ban on all geese has been in operation in the last years (Iliev et al., 2020). General regulations of hunting periods and quotas reduced hunting territories, and development of a license system for goose hunting and control have also been implemented at key staging sites since 2010 (Rozenfeld, 2011). Altogether, these conservation measures may have prevented the population from further decline by improving conditions at the staging and wintering areas. In addition, the potential increase in survival probabilities may be linked to the increased abundance of some greater white-fronted goose *Anser albifrons* populations, which partially share the Asian route with the Fennoscandian lesser white-fronted goose and are commonly hunted (Fox and Leafloor, 2018; Jones et al., 2017). Increased abundance of these geese populations may have resulted in a

dilution effect, reducing the average probability that any Fennoscandian lesser white-fronted goose will be harvested when a higher number of other geese are present at the same time.

Out of all demographic parameters, winter adult survival seemed to be affected most strongly by the onset of predator control in 2008 on average ($\beta_{management.S2}$ in Fig. 6). Ideally, we would have quantified its contribution to the change in realized population growth rate after 2008 (e.g., through a transient Life Table Response Experiment, Koons et al., 2016) and compared it to the contribution of the other parameters, but preliminary tests revealed that the uncertainty in our estimates is far too large for such an analysis to be informative. Thus, we cannot conclude that winter adult survival was more important than the other vital rates to invert the declining population trend. Moreover, winter survival here is partly confounded with survival during migration between Greece and Hungary because we used a single maximum count for the wintering period in Greece. From a practical point of view, the fact that the estimates of all the survival probabilities that were allowed to vary in the model may have increased after 2008 suggests that a comprehensive approach, with conservation actions implemented at different stopovers along the entire migration flyways as well as in the breeding and wintering areas, may be key to ensure the conservation of this small population. Because reproductive success is tightly linked to small rodent population cycles in northern Fennoscandia through the alternative-prey mechanism (Marolla et al., 2019) and the cycles of some rodent species are becoming more irregular (Cornulier et al., 2013; Kausrud et al., 2008; Nolet et al., 2013), ensuring protection at key staging, wintering, and breeding sites of the population in good reproductive years may be fundamental to increase recruitment and thereby population size. Indeed, the goose population experienced abrupt increases in size following good reproductive years in the period when conservation actions were already in place.

Previous studies have shown that, with the type of inverse modelling that we used, estimating between-year variability in survival is possible (e.g. Gross et al., 2005; Link et al., 2003). Nonetheless, we were unable to estimate temporal variability in the demographic parameters due to the relatively sparse data in our study. This might be an important limitation, especially considering the large between-year variability in breeding success in the lesser white-fronted goose population that fluctuates with the rodent cycles (Marolla et al., 2019). We believe that the lack of data from Greece in the period 1998–2004 in the model, combined with the lack of information on stage-structure in Hungary and the fact that yearlings are only distinguished in Norway, has increased the uncertainty of the parameters. In integrated population models (Schaub and Abadi, 2010; Schaub and Kéry, 2022), most of the information to estimate apparent survival probabilities tends to come from capture-recapture data, and such data are not available for this critically endangered goose population. We expect to get more accurate estimates when more years of stage-structured count data are available.

4.1. Conservation and management implications

Evaluating the effectiveness of conservation/management actions on small populations is challenging, because proper experiments designed to include controls as well as temporal and spatial replications of actions are usually not achievable (Taylor et al., 2017). Removing or controlling predators is often beneficial to declining bird populations, but unsuccessful programs are frequent (Dicks et al., 2019; Williams et al., 2019; Jiguet, 2020). Based on a management design including spatial contrasts, it has been shown that culling of red foxes likely contributed to increasing the population density of willow ptarmigan *Lagopus lagopus* in northern Norway (Henden et al., 2021). Moreover, red fox culling likely contributed to prevent local extinction of the arctic fox *Vulpes lagopus* (Ims et al., 2017). However, using both food-web analysis (Marolla et al., 2019) and state-space modelling of the realized population dynamics (this study), we were unable to find any evidence for a contribution of fox culling to the recent increase in abundance of the

Fennoscandian lesser white-fronted goose population. In Marolla et al. (2019), we discussed that compensatory immigration (Lieury et al., 2015; Newsome et al., 2014), compensatory effects of other nest predators (Henden et al., 2014; Parker, 1984), and insufficient culling may all explain the apparent lack of influence on goose reproductive success. A potential change in age distribution after the population increased, with potentially younger breeding pairs that produce smaller broods (Raveling, 1981; Conover, 2012; Koons et al., 2016), might also have masked the effects on breeding success. Here, we found that red fox culling seems to have reduced early breeding failure and thereby the proportion of birds that embark on a longer migration through western Asia. This, however, appears to not have contributed much to the population recovery, because adult goose survival hardly seems to differ between the European and the Asian migration routes – although statistical uncertainty and potential compensatory immigration from the neighbouring Russian population of lesser white-fronted goose precludes definitive conclusions. Still, we found indications that the remarkable effort of implementing conservation actions in several countries to ensure population protection throughout the annual cycle may have been beneficial to the targeted lesser white-fronted goose population. That population dynamics at non-breeding sites can be as or even more important than the dynamics at breeding sites is being increasingly acknowledged (Hostetler et al., 2015; Marra et al., 2015). It is therefore plausible that increased safety at staging and wintering sites combined with improved habitat conditions has ensured high survival and recruitment, and that this has been particularly important in years with high reproductive success.

In this respect, it will be important not only to continue the monitoring at the currently surveyed staging sites, but also to include new locations in the monitoring scheme. For instance, the implementation of a systematic monitoring program at important bird areas in northern Kazakhstan has been proposed after a full-scale survey, with a stratified site sampling, was conducted in 2016 (Cuthbert et al., 2018). Including such data in the demographic model we have developed in this study could help disentangle whether a certain leg of the Asian route is affected by higher goose mortality. Another aspect of the model that could be improved in the near future is the partial confounding between survival during the migration between Hungary and Greece and survival during wintering in Greece. Using daily count data will allow defining a winter period that does not overlap with migration. Moreover, we encourage making age-structured counts whenever possible. In staging areas where these data are difficult to obtain such as in Hungary, even having the age-structure for a random sample of birds may greatly aid at getting better parameter estimates. We believe that iterating both the demographic analysis and the management evaluation over the coming years will be crucial to optimize the approach further and to better understand whether the flyway conservation tactic adopted for the Fennoscandian lesser white-fronted goose is actually preventing the extinction of the population or increases its rate of recovery. In the meanwhile, continuing the present combination of cross-national efforts is likely the best conservation strategy.

CRediT authorship contribution statement

F. Marolla, S. Hamel, and N. G. Yoccoz conceived the idea; F. Marolla, M. Kéry, and M. Schaub designed the modelling strategy; T. Aarvak, I. J Øien, and M. Vougioukalou provided goose count data; R. A. Ims and N. G. Yoccoz provided data on small rodent abundance; F. Marolla organized the data; F. Marolla and C. R. Nater analyzed the data; F. Marolla led the writing of the manuscript. All authors contributed critically to the writing of the manuscript. None of the authors has conflict of interest to declare.

Declaration of competing interest

We confirm that this manuscript is all original research carried out

by the authors and has not been published elsewhere and is not under consideration by other journals. All authors have approved the manuscript and agreed with its submission to Biological Conservation. All persons entitled to authorship have been included. All sources of funding are acknowledged in the manuscript. All work conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare, and to the Journal's policy on these matters. We have no conflicts of interest to disclose.

Data availability

The R code to generate the data and the JAGS code to run the model is available as Supplementary Material.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110028>.

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