Population Models: Flexibility, Advances, and Applications to Wildlife Conservation. The Bonelli’s Eagle as a Study Case

Jaume Adrià Badia Boher

POPULATION MODELS: FLEXIBILITY, ADVANCES, AND APPLICATIONS TO WILDLIFE CONSERVATION.

THE BONELLI'S EAGLE AS A STUDY CASE.

Jaume A. Badia-Boher

UNIVERSITAT DE
BARCELONA

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Universitat de Barcelona
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
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Population Models: Flexibility, Advances, and Applications to Wildlife Conservation.

The Bonelli's Eagle as a Study Case

Memòria presentada per Jaume Adrià Badia Boher per optar al grau de Doctor per la Universitat de Barcelona

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Jaume Adrià Badia Boher
El doctorand

Vist-i-plau dels directors i el tutor de la tesi:

Dr. Joan Real Ortí
Director i tutor de la tesi

Dr. Antonio Hernández Matías
Codirector de la tesi

The Bonelli's eagle

Aquila fasciata

The Bonelli's eagle has a fragmented Distribution across the Southern Paleartic and Indomalayan regions. It is locally rare and in decline across its range. In western Europe, the species has a generally continuous distribution from southern France and across the Mediterranean coast to southern Portugal, although its range becomes patchy at the western and northern edges. Some populations can also be found in Mediterranean islands: Mallorca, Sardinia, Sicily, Crete, and Cyprus. The eagle's prey mainly includes small or medium-sized birds and mammals, along with some reptiles and insects. It may be found nesting on remote cliff ledges or in large trees.

White coloured breast with a variable amount of sparse blackish-brown streaks

Wing tips moderately fingered for such a large raptor

Grey tail with obscure darker brown thin bars and a broad black terminal band

"The most exciting phrase to hear in science, the one that heralds new discoveries, is not "Eureka!", but "That's funny".

Isaac Asimov

"All models are wrong, but some are useful".

George E. P. Box

"I feel like I'm nothing without wildlife. They are the stars. I feel awkward without them".

Bindi Irwin

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Abstract

In this thesis, we took advantage of recent advances in the degree of sophistication and flexibility of population models to study the population dynamics and conservation of long-lived species. As main objective, we aimed at understanding the effects of permanent emigration in the estimation of survival from mark-recapture analyses and its multiple implications for the interpretation of population dynamics and the reliability of population viability projections. In second term, we aimed at generating evidence-based knowledge based on quantitative population analysis to guide the management of long-lived raptors. To address these issues, we used two populations of the long-lived Bonelli's eagle as study cases (Catalonia and Mallorca, western Mediterranean), for which extensive demographic and ecological data were available. The thesis was divided into the four following chapters.

In *Chapter 1*, we implemented individual-based population viability analyses (PVA) to evaluate the effectiveness of different release strategies used in the reintroduction of the Bonelli's eagle in Mallorca. Our results suggested that relocating wild-reared non-juvenile raptors from natural populations to reintroduction areas may better favour reintroduction success in comparison to more expensive, widely implemented alternatives based on captive breeding. The better performance of relocations was related to their capacity to promote early reproduction in the reintroduction area, which may enhance population growth.

In *Chapter 2*, we developed a spatially-explicit capture-mark-recapture model adapted to the multistate formulation to separate true survival and permanent emigration in long-lived species. In addition, we compared the obtained stage-structured true survival estimates to apparent survival estimates. Our results showed that the magnitude of the differences between true and apparent survival may vary across population stages in long-lived species (i.e., age, sex, breeding status) because of intrapopulation variation in the effect of permanent emigration. In addition, our findings suggested that the use of heavy-tailed distributions to model natal dispersal may provide more effective separations of true survival and permanent emigration in cases of mark-recapture data limited to restricted study areas.

In *Chapter 3*, we integrated the model developed in chapter 2 into a spatially-explicit Integrated Population Model (SEIPM) aimed at insightfully describing the long-term dynamics of the Bonelli's eagle population in Catalonia (1986-2020) and extracting relevant knowledge for long-lived species demography. The use of SEIPMs enabled an explicit estimation of emigration, immigration, and sink-source status along time, together with key demographic parameters and the dynamics of relevant population stages. Our results allowed a deep understanding of the retrospective dynamics of the study population and revealed new insights about the long-term variations of sink-source status and floater populations in long-lived species.

In *Chapter 4*, we used the estimates of apparent and true survival from chapter 2 to compare the outcomes of PVAs using both types of estimates and their respective fits to census data. In addition, we explicitly modelled emigration and immigration to evaluate how these processes may improve or decrease the fits of PVAs based on each type of survival estimate. Our results suggested that each of both survival types may only provide accurate PVA projections in specific population scenarios where emigration and immigration match the particularities of each type of estimate. Thus, we emphasized the importance of either modelling migration processes or using calibration to real data for accurate PVA outcomes.

In conclusion, this thesis provided useful extensions of demographic models for the estimation of true survival and the fine-scale study of population dynamics in long-lived species. In addition, important insights were revealed about the reliability of PVA outcomes relative to the characteristics of survival estimates. Finally, the thesis emphasized the relevance of generating evidence-based knowledge from the analysis of quantitative data for conservation decision-making.

Sinopsi

Aquesta tesi utilitza els avenços recents en el grau de sofisticació i la flexibilitat dels models poblacions per a generar coneixement rellevant per a l'estudi de la dinàmica de poblacions i la conservació d'espècies de vida llarga. Com a objectiu principal, la tesi se centra en entendre els efectes de la migració permanent en l'estimació de supervivència en anàlisis de captura-recaptura, així com els efectes que això pot tenir per a la interpretació de la demografia, les estimes de viabilitat, l'estat de conservació i la gestió de les poblacions de vida llarga. En segon pla, la tesi se centra en generar coneixement basat en evidències quantitatives per guiar la gestió d'aus rapinyaires de vida llarga. Per afrontar aquests objectius, hem utilitzat com a casos d'estudi dues poblacions de l'àliga perdiguera (Catalunya i l'illa de Mallorca), de les quals es disposa d'una extensa quantitat de dades de seguiment demogràfic i ecològic. La tesi s'ha dividit en els següents capítols:

Al *Capítol 1*, es van desenvolupar anàlisis de viabilitat poblacional basades en individus (PVA) per avaluar l'efectivitat de les diferents estratègies d'alliberament emprades en la reintroducció de l'àliga perdiguera a Mallorca. Els resultats suggerien que la translocació d'individus no-polls salvatges d'altres poblacions cap a l'àrea de reintroducció afavoria l'èxit de la reintroducció en comparació amb altres metodologies més cares basades en la cria en captivitat. Aquesta major efectivitat estava lligada a la capacitat de les translocacions de no-polls d'accelerar una ràpida reproducció a l'àrea d'estudi, fet que promovia un ràpid creixement poblacional.

Al *Capítol 2,* vam desenvolupar models de captura-recaptura espacialment explícits adaptats a la formulació multi-estat per estimar separadament supervivència real i migració permanent en espècies de vida llarga. Les estimes de supervivència real obtingudes, estructurades per fracció poblacional, van ser comparades amb estimes de supervivència aparent. Les comparacions mostraven que aquestes diferències variaven en intensitat al llarg de les diferents fraccions (edat, sexe, estat reproductor) degut a variacions intrapoblacionals en l'efecte de la migració permanent. Per altra banda, els nostres resultats suggereixen que l'ús de distribucions estadístiques de cua ampla per modelar dispersió natal poden ajudar a separar supervivència real i migració permanent de manera més efectiva quan les dades disponibles sobre captura-recaptura estan restringides a l'àrea d'estudi.

Al *Capítol 3*, vam incorporar el model desenvolupat al capítol 2 dins un model integrat poblacional espacialment explícit (SEIPM) amb l'objectiu de descriure detalladament la dinàmica de la població d'àliga perdiguera a Catalunya durant les darreres quatre dècades (1986-2020), i extreure coneixement general rellevant sobre la demografia de les espècies de vida llarga. L'ús de SEIPMs va permetre una estimació explícita dels processos d'immigració i emigració, així com de l'estat font-embornal de la població al llarg del temps, juntament amb paràmetres demogràfics clau i la dinàmica d'importants fraccions poblacionals. Els resultats van permetre entendre detalladament la dinàmica retrospectiva de la població, i van revelar nous aspectes sobre la demografia de les poblacions flotants i les dinàmiques font embornal a llarg termini.

Al *Capítol 4*, vam emprar les estimes de supervivència aparent i real del capítol 2 per comparar els resultats de PVAs basats en ambdós tipus d'estimes i el respectiu ajust de cada model a dades reals de cens. A més, vam modelar de manera explícita emigració i immigració per avaluar com aquests dos processos poden millorar o empobrir l'ajust dels models basats en els dos tipus d'estima de supervivència. Els resultats mostraven que ambdues supervivències només tenien capacitat de generar estimes precises de viabilitat en escenaris poblacionals específics on els processos d'emigració i immigració tinguessin unes magnituds molt concretes. En conseqüència, vam subratllar la importància de modelitzar processos migratoris dins els PVAs - o bé de calibrar els resultats amb dades reals - per millorar la fiabilitat d'aquests models.

En resum, en aquesta tesi s'han desenvolupat extensions de models poblacionals per a l'estimació de supervivència real i l'estudi detallat de les dinàmiques poblacionals en espècies de vida llarga. A més, la tesi ha aportat troballes importants sobre la fiabilitat i la precisió dels PVAs segons les particularitats de les estimes de supervivència emprades. Finalment, s'hi ha destacat la importància de generar coneixement basat en l'evidència científica per a la gestió de poblacions salvatges a través de models poblacionals.

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GENERAL INTRODUCTION

Photograph courtesy of Jaume Elies

Population models in context

Understanding how and why wild populations change in size and structure is a crucial concern in ecology, as it allows to comprehend and predict the complex interactions between species and their environments. The study of population dynamics involves analysing the changes in the number, distribution, and composition of populations over time. This information is fundamental for understanding the underlying ecological mechanisms that affect population growth, decline, and stability (Price & Hunter, 1995). The insights gained from population dynamics research are also central for wildlife conservation (Morris & Doak, 2002). The threats that affect animal populations are diverse, from habitat loss to climate change and nonnatural mortality from anthropogenic sources. Without a thorough understanding of population dynamics, we risk making uninformed management decisions that could have negative consequences for ecosystems and the species that depend on them (Sutherland et al., 2004a; Martínez-Abraín & Oro, 2012). Population models have taken a fundamental role in the study of population dynamics and wildlife management. These analytical tools permit testing for different ecological hypotheses or conservation scenarios without the need to explicitly alter natural conditions in wild populations (Morris & Doak, 2002; Kéry & Schaub, 2012). Overall, population models allow to estimate demographic parameters (e.g., Lebreton et al., 1992; Hernández-Matías et al., 2011a), predict the effects of environmental change on population dynamics (e.g., Keith et al., 2008; Hoffman & Sgrò, 2011; Jenouvrier, 2013), evaluate the effects of different management or conservation strategies on population dynamics and identify those that may be most effective (e.g., Walsh et al., 2012; Saunders et al., 2018), assess conservation status in threatened populations (e.g., García, 2003; Rhodes et al., 2010), and describe the trends of populations in the short, mid, and long terms (e.g., Hernández-Matías et al., 2013; Margalida et al., 2020).

A general problem in the study of wild populations is that the observation of ecological and demographic processes is often incomplete or imprecise. For example, censuses and surveys will easily miss some or most individuals in a population because their detection probabilities are often lower than one; or may even incur into erroneously counting the same individuals more than once (Kéry & Schaub, 2012; Kellner & Swihart, 2014).

Consequently, data from natural populations are generally obtained from small samples and may be subject to different sources of bias. These particularities must be treated with specific sampling protocols and statistical treatments in order to infer reliable conclusions of the status and dynamics of study populations (Sutherland et al., 2004b; Zuur et al., 2007). With this aim, there have been considerable advances in the degree of sophistication of these protocols and analytical methods over the last decades. An important milestone was the development of the capture-mark-recapture methods (CMR) and the corresponding statistical formulations to analyse the resulting data in the famous Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965). The first CMR methods allowed for the estimation of key demographic parameters in marked populations, such as population size, survival, and recapture probabilities while accounting for the common issue of imperfect detection (Lebreton et al., 1992). Between the 1970s and the early 2000s, several advances provided further sophistication to CMR methods to account for a wider range of population processes and heterogeneities. For instance, at the beginning of the 1990s, Burnham (1993) provided a framework to consider recoveries of dead individuals in CMR models, which allowed for a more precise estimation of demographic parameters. Another considerable advance was the development of the multistate formulation, which provided a straightforward design to account for heterogeneity in detection and survival probabilities among individuals, age classes, sex, and population stages (Lebreton and Pradel 2002; Lebreton *et al.*, 2009). In addition, multistate models allowed for an easy consideration of further key demographic parameters, such as recruitment to adult or breeding populations, and movement probabilities between populations or study sites (Lebreton et al., 2009; Hernández-Matías et al., 2011a). More recently, multievent models provided a design to account for uncertainty in state assignment when field observations do not necessarily correspond to the underlying states of the individuals (Pradel, 2005). Multievent models have proved useful at dealing with uncertainty in the assessment of sex (Genovart et al., 2012), causes of death (Fernández-Chacón et al., 2017), or breeding status (Richard et al., 2017). The spread and growth in popularity of CMR modelling would not be understandable without the development of software that permitted users without a very strong statistical background to familiarise and make use of these methods, such as the programmes

MARK, M-SURGE, and E-SURGE (White & Burnham, 1999; Choquet et al., 2004, 2009).

The rapid development of mark-recapture methods in the last decades has come alongside that of population viability analyses (PVA; Boyce, 1992). PVAs encompass a wide range of population models mainly aimed at predicting the likely future status of a population or collection of populations of conservation concern, although these models have also been used to study the retrospective dynamics of populations (Morris & Doak, 2002). By modelling population dynamics and potentially accommodating a wide range of factors that affect population viability, PVAs can help identify key drivers of population decline or extinction risk and evaluate the potential effectiveness of management strategies (Bakker & Doak, 2009). From the first PVAs that estimated population growth rates based on count data, these analytical tools rapidly evolved in sophistication and flexibility, which progressively enabled a more accurate representation of population heterogeneity and demographic and environmental stochasticity (Dennis et al., 1991; Elderd et al., 2003). In this respect, the conception of demographic PVAs (also known as stage-structured PVAs; Holmes, 2001; Morris & Doak, 2002) was an important step forward. These models allowed for a more detailed representation of the study species life cycle and delivered probabilistic estimates of extinction risks based on survival and reproduction data for each life stage of a population (i.e., different age classes, breeding status, or sex, among others). Importantly, the stage-structured survival estimates needed to implement stage-structured PVAs are generally obtained from CMR analyses (Bradshaw et al., 2013). Hence, many important advances in the study of population dynamics have been the result of the combination of both methods. In addition, demographic PVAs often include so-called sensitivity analyses, which evaluate how sensitive one variable is in the model (generally the population growth rate, also known as lambda) to changes in another variable (Beissinger & Westphal, 1998). Sensitivity analyses have allowed a deep understanding about the general importance of survival in determining population growth, especially adult or breeder survival in long-lived species (Saether & Bakke, 2000). Besides, this relevant knowledge helped managers at promoting conservation actions targeted at increasing adult survival in order to effectively revert population declines in threatened long-lived species (Heppell, 1998; Badia-Boher et al., 2019). Further developments in PVAs have allowed to consider space (spatial PVAs) or multiple populations and their interactions (metapopulation PVAs) into viability predictions (Hernández-Matías et al., 2013; Fryxell et al., 2020; Folt et al., 2021). Although these last methods are very data hungry and require explicit data about dispersal processes and often survival variation over space or over populations, they may provide very useful insights on the functioning of metapopulation systems and the implementation of conservation action in specific areas of a population's range.

In the field of wildlife conservation, the development of PVAs is providing an opportunity to move from the traditional management conducted from a "feel-belief" basis to relying on more objective, quantitative measurements. Because of this, the use of PVAs has been promoted by influential organisations, such as the International Union for the Conservation of Nature (IUCN) in its Red List Criteria (IUCN, 2008), and the Government of the United States of America in the Endangered Species Act (ESA; United States of America, 1983). In addition, the development of user-friendly computer software programmes has further contributed to the proliferation of PVAs (Lacy, 1993; Mills & Smouse, 1994). Parallel to the popularisation of these methods, considerable research efforts have been devoted to investigating their potential weaknesses and limitations, especially those of demographic PVAs as they are used most often (Beissinger & Westphal, 1998; Reed et al., 2002; Himes Boor, 2014; Chaudhary & Oli, 2020). Based on this research, two main criticisms are often pointed out. The first is that PVAs are often used to calculate extinction risks of rare, threatened, and/or fragmented populations, for which available data may not be of sufficient quality. Since these species often have small population sizes, it is difficult to obtain enough detailed data to accurately estimate key demographic parameters such as survival or productivity. Because these vital rates are the basis of demographic PVAs, large parameter uncertainties may propagate into model calculations and lead to highly uncertain predictions. In this scenario, model results may be practically meaningless in a management context. A second criticism is that the life cycles of rare or understudied species are sometimes not known with certainty. The robustness of demographic PVAs relies on an adequate modelling of the life cycle of a study species, as one must define a specific number of population stages and relationships among them from which model calculations are drawn. There are other demographic and statistical processes that should not be obviated in the PVA structure, as they can have significant impacts on the assessment of extinction risks. This is the case of environmental and demographic stochasticity (Engen et al., 1998). Environmental stochasticity refers to unpredictable spatiotemporal fluctuations in environmental conditions, which may result in variations in key demographic parameters. Demographic stochasticity describes the random fluctuations in population size that occur because the births and deaths of each individual are discrete and probabilistic events. Density-dependence is another relevant process to be considered in PVAs, as it can slow down declines in small populations but also limit population growth in some circumstances (Henle et al., 2004). Obviating any of these processes in PVA structures may lead to biased model predictions, which may end up in inadequate population management decisions.

Bayesian population models: advances and opportunities for the study of population dynamics

The recent popularisation of Bayesian methods in ecology and conservation is having a significant impact on the modelling of wild populations (Royle & Dorazio, 2008; Kéry & Schaub, 2012; Kéry and Royle, 2015). The development of flexible R languages such as BUGS (Bayesian inference Using Gibbs Sampling) and Stan has allowed ecologists to implement complex Bayesian models without the need for a strong statistical background (Gilks et al., 1994; Gelman et al., 2015). Importantly, these languages allow for the construction of hierarchical models (also known as multilevel models; Royle & Dorazio, 2008; McElreath, 2019). These are particularly useful for modelling ecological and population dynamics systems in detail, as they allow to break down complex stochastic processes into a dependent sequence of simpler submodels with their associated variabilities. This partitioning may be beneficial for a better understanding of the modelled system, for computational ease, and for an honest accounting for all levels of uncertainty in the system. In addition, thanks to their flexibility, hierarchical models permit a more straightforward construction of difficult models, including some that cannot be fitted in classical frameworks (Kéry & Schaub, 2012; Schaub & Kéry, 2021). Because of these reasons, hierarchical models are being increasingly used in ecological and population models. Bayesian models also allow the integration of prior knowledge and data to make more accurate predictions about specific parameters (Wesner & Pomeranz, 2021). This is especially useful in cases where the data available for parameter estimation are limited or scarce, which may happen frequently in ecological systems. Because of all these reasons, the use of Bayesian models in CMR analyses has also grown rapidly in recent years (Calvert et al., 2009; Kéry & Schaub, 2012).

One more crucial aspect of Bayesian hierarchical models and the BUGS language is their ease and flexibility at integrating multiple data types into statistical models. This has favoured the popularization of Bayesian Integrated Population Models (IPMs; Besbeas et al., 2003; Schaub & Abadi, 2011). Importantly, IPMs are generating a new paradigm in the analysis of wild populations. In conventional approaches, key vital rates are first estimated from analyses of single data sources, such as CMR analyses for survival and recruitment, productivity estimates from fecundity data, or population counts from census data (Figure 1). In a second step, models of population dynamics are designed – most often PVAs – to model the future or retrospective demographic trends of a population (Morris & Doak, 2002). In contrast, Integrated Population Models integrate demographic data from multiple data sources to jointly estimate key demographic parameters over time, such as population size, survival, recruitment, and productivity, while accounting for all sources of uncertainty (Plard et al., 2019; Figure 2).

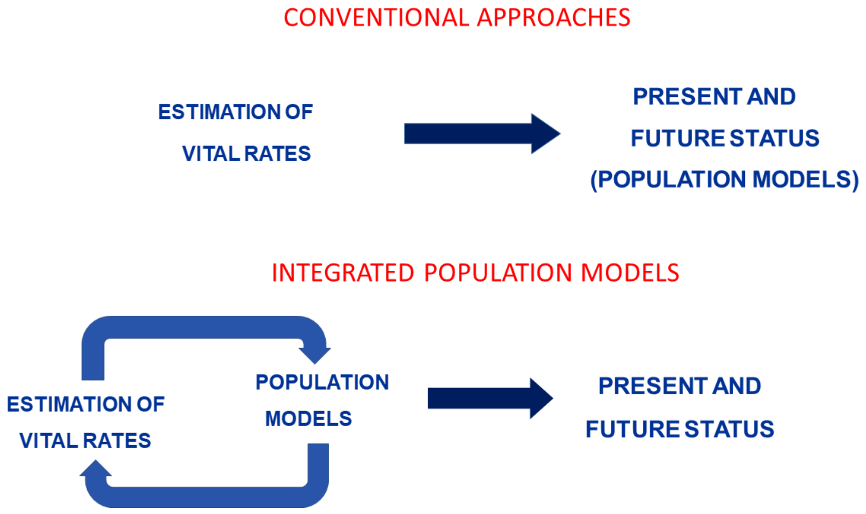

Figure 1. Differences in the analysis of wild populations between conventional approaches and Integrated Population Models (IPMs).

One advantage of IPMs is that demographic parameters are more precisely and accurately estimated compared to inferences from single data sources (Besbeas et al., 2002; Schaub and Abadi, 2011). IPMs can even estimate demographic parameters when there are no explicit data about them by using indirect information contained in other data sources (Abadi et al., 2010). While IPMs are often used to study retrospective population dynamics, they can be easily extended to forecast the fate of a population over time (Schaub & Kéry, 2021). IPMs can easily integrate every type of CMR model, from CJS to multistate and multievent along with further extensions (e.g., Kéry & Schaub, 2012; Jan et al., 2017; Margalida et al., 2020). Although the uses of IPMs are wide, these models have proven especially useful at understanding the effect of environmental variables on population dynamics (e.g., Abadi et al., 2010; Weegman et al., 2017), detailing fine-scale population dynamics of multiple population stages (e.g., Margalida et al., 2020; Hostetler, 2021), unveiling cryptic population declines (Oppel et al., 2022), exposing causes of population decline and viability drivers (Brooks et al., 2004; Schaub et al., 2010), and evaluating the effectiveness and guiding the use of different management actions (Millsap et al., 2022).

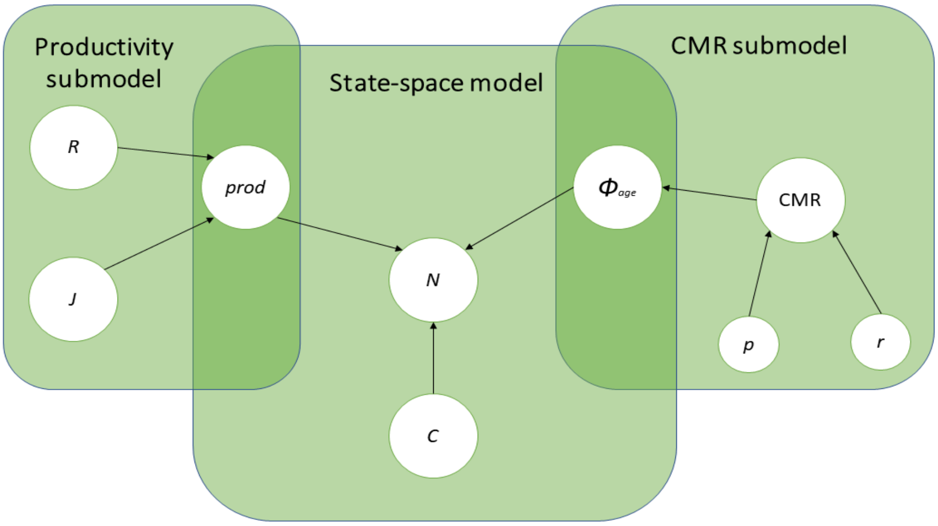

Figure 2. General structure of an Integrated Population Model (IPM). In the productivity submodel, productivity (prod) is estimates from data consisting of the numbers of breeders from which reproduction is monitored, and the numbers of individuals born. The capture-mark-recapture (CMR) submodel estimates recapture (p) and recovery (r) parameters along with age-structured survival (Φ_{age}). Using survival and productivity data along with population counts (C), the state-space model estimates population size.

The flexibility of Bayesian hierarchical models has also favoured recent developments in spatially-explicit CMR models (SECR; Chandler & Clark, 2014; Schaub & Royle, 2014). SECR models permit including spatial processes in CMR models, such as spatial variation in demographic parameters like survival or detection probabilities, animal movement, migration, and dispersal in a variety of ways. These developments can constitute crucial advances for the study of population dynamics. Indeed, the role of dispersal processes in shaping the demography of a population is acknowledged in a wide range of ecological fields (Clobert et al., 2012; Hernández-Matías et al., 2013; Kubisch et al., 2014; Paquet et al., 2020). From a basic perspective, population dynamics are composed of the so-called four BIDE processes: Birth, Immigration, Mortality, and Emigration (Levin et al., 2009). Any changes in population dynamics over time must be due to changes in any of these components. Nevertheless, most studies of population dynamics have only focused on birth and mortality processes using productivity and survival data and without an explicit modelling of migration fluxes (Morris & Doak, 2002). Although this decision is often made for practical reasons as obtaining reliable dispersal data of study populations has traditionally been difficult, it also means ignoring two BIDE processes with a fundamental role in shaping population dynamics, which may lead to a poor understanding of the status and regulation of populations (Schaub et al., 2010; Mihoub et al., 2011; Furrer & Passinelli, 2016; Millon et al., 2019). In addition, ignoring migration processes in CMR analyses – particularly emigration – may also have strong implications for survival estimations (Marshall et al., 2004; Horton & Letcher, 2008). In this respect, an important assumption of mark-recapture methods is that there cannot be any emigration from the study area. The presence of emigration may lead to potential biases in survival and recapture estimates. Particularly, if emigration is temporary and random, detection probabilities may become biased (Fujiwara & Caswell, 2002). Instead, if emigration is permanent (that is, if individuals that leave the study area will not return), models cannot distinguish between mortality and emigration, which may lead to underestimations of survival (Marshall et al., 2004; Schaub & Royle, 2014). Importantly, permanent emigration is a common phenomenon in mark-recapture studies, mainly due to two facts. First, study areas for demographic studies are finite in size and rarely cover whole biological populations or species distributions (Horton & Letcher, 2008; Chadoeuf et al., 2017). Hence, individuals that just move across the range of a population may eventually abandon a study area and thus become indetectable to mark-resighting schemes. Second, the main driver of permanent emigration is natal dispersal, that is, dispersal from an individual's area of birth to the area of first breeding (Benton and Bowler, 2012). Natal dispersal comprises the largest movements in an individual's lifetime in the vast majority of animal species (Clobert et al., 2012). In many populations, natal dispersal movements can reach considerably large distances that can easily exceed the limits of study areas (Zimmermann et al., 2007; Horton & Letcher, 2008; Fandos et al., 2023). Given the high recurrence of permanent emigration in mark-recapture studies, survival estimates have often been presented as apparent survival, which is the product of true survival and study site fidelity (Lebreton et al., 1992; White & Burnham, 1999). Whenever permanent emigration is present in the study area, site fidelity is lower than 1, leading to differences between the true and apparent estimates of survival. The use of apparent survival in CMR models is widespread. In most cases, apparent survival is estimated for convenience, as data requirements and analytical tools to separate mortality from permanent emigration can be complex (Zimmermann et al., 2007; Gilroy et al., 2012). However, drawing conclusions about population status and dynamics based on apparent survival may be problematic. First, apparent survival has no clear biological meaning and if estimated with time, sex or age variations, differences between population stages may correspond to actual variations in dispersal behaviour and not to true survival differences (Marshall et al., 2004; Schaub & Royle, 2014). Second, it appears logic that if apparent survival is used for models of population dynamics, such as IPMs or PVAs, population trends may be underestimated or different parameters may be biased, especially if differences between true and apparent survival are large (Lieury et al., 2016; Riecke et al., 2019). Nevertheless, even with these potential issues, the effect of permanent emigration in apparent survival and subsequent effects on demographic models or result interpretations is mainly overlooked in ecological studies. For instance, Zimmermann et al. (2007) reviewed 82 studies based on apparent survival in top-ranked ecology and ornithology journals and found that none acknowledged or discussed the potential effects of permanent emigration. Therefore, there is an urgent need to 1) understand how permanent emigration may affect survival estimation in study populations, and 2) develop accessible, more widely implementable tools to enable a separation of true survival from the effects of permanent emigration.

The development of Bayesian hierarchical SECR models can provide proficient tools to tear apart true survival from permanent emigration. For instance, Schaub & Royle (2014) provided a promising formulation to jointly estimate survival and dispersal data from marked populations in the Cormack-Jolly-Seber model. In parallel, Ergon and Gardner (2014) created a similar framework adapted to the CMR robust design. Additionally, Terui (2020) proposed an extension for habitats that could be simplified to a linear space, such as water flows. However, spatially explicit CMR models for the estimation of true survival still require considerable advances to be generalisable to multiple species and population types. The seminal works of Schaub & Royle (2014) and Ergon & Gardner (2014), and their extensions (Paquet et al., 2020) have mainly focused on relatively short-lived species, such as passerines and micromammals. Instead, long-lived species have remained mainly overlooked to date, although understanding the effects of survival biases on their population dynamics may be essential for their study and conservation.

The role of Bayesian population analyses in addressing challenges in the study of long-lived species population dynamics

Long-lived species are those with long life expectancies, delayed sexual maturity, and low reproductive rates. Due to their slow life cycles, these may have a reduced ability to respond to environmental change or disturbance. Hence, they are particularly vulnerable to human-related mortality and a considerable fraction of them are currently endangered or declining (Saether & Bakke, 2000; Webb et al., 2002; Keevil et al., 2018). In addition, long-lived species are often considered flagship or umbrella species whose conservation can benefit whole ecosystems (Roberge & Angelstam, 2004; Miralles et al., 2019). Because of these reasons, these species are common targets of conservation action (Cardoso et al., 2011). Gaining a deep understanding about long-lived population dynamics is crucial to implement effective management. However, this is particularly challenging mainly because of two factors. First, due to their long lifespans, monitoring and mark-resighting schemes need to be performed for many years or even decades to cover multiple generations of study species. In addition, since population sizes of long-lived species are often small due to both their slow life cycles and generally poor conservations statuses, monitoring programmes must be intensive in order to obtain large enough sample sizes for precise estimations of demographic parameters (e.g., Badia-Boher et al., 2019; Margalida et al., 2020). Overall, obtaining the necessary data to study these species is both time and resource consuming. The second concern is that long-lived species show complex population dynamics, and hence fine-scale statistical models are required to unveil their functioning and drivers (Gimenez et al., 2018). Such complex dynamics arise from their complex behavioural patterns (e.g., foraging strategies, movement patterns, territoriality), which usually vary with age and/or across both sexes, local populations, or individuals (Sergio et al., 2014). For instance, individuals may improve their hunting or predatory avoidance skills with age, which may increase their chances of surviving along time (e.g., Hernández-Matías et al., 2011a). Animals may frequent different habitats depending on their age, sex, or breeding status, which may affect their detection probabilities, risk exposures to different mortality threats, and dispersal probabilities (Cubaynes et al., 2010; Hernández-Matías et al., 2011a; Penteriani et al., 2011; Badia-Boher et al., 2019). Territorial behaviour or parental care may be equal or inequal among sexes, which may lead to survival differences between sexes (Toïgo & Gallard, 2002; Nichols et al., 2004). Overall, long-lived species usually present large intrapopulation heterogeneities in demographic parameters. As a result, we need complex models that structure these populations in different stages to accommodate these levels different levels of heterogeneity.

Precisely, the complex behaviours of these species, with differences in movement, foraging, and dispersal patterns, may lead to complex variations in the likelihood of permanent emigration among population stages. Consequently, if conventional CMR methods to estimate apparent survival are used, it might not be possible to distinguish whether survival differences between population stages are due to actual differences in true survival or differences in permanent emigration. This is potentially conflictive because stage-specific demographic parameters of long-lived species, such as age-specific survival estimates, can have considerably different effects on population growth rates (Saether & Bakke, 2000). Thus, tearing apart true survival from permanent emigration may favour the design of specific conservation actions that promote population growth, and improve our understanding of the dynamics of long-lived populations. In this scenario, SECR models could be a flexible, widely applicable solution to this issue. However, these models have been scarcely implemented in long-lived species to date, probably because adapting them to their demographic particularities entails complex modelling challenges. First, to accommodate their typically large levels of intrapopulation heterogeneity in survival and dispersal parameters along with other population processes, SECR models should be adapted to the multistate capture-recapture formulation. The second challenge has to do with the complexity of natal dispersal processes in many populations of long-lived species. As in other species, long-lived animals mainly undertake the longest movements in their lives – and hence those that most probably can result in permanent emigration – right before first breeding (i.e., natal dispersal). However, long-lived species show deferred sexual maturity, and it may take several years for individuals to become breeders (Margalida et al., 2020). In addition, in many species the age of first breeding is not determined at a fixed age, but rather varies between individuals, sex, and even along time as a response to density-dependence processes (Hernández-Matías et al., 2010; Morandini et al., 2019). Hence, the patterns of stage-specific site fidelity, and corresponding differences between apparent and true survival, may largely vary between species, populations, or even time periods in the same population. Therefore, for an accurate separation of true survival and permanent emigration, it is essential to estimate the age of first breeding as a stage-structured parameter and couple its modelling to that of natal dispersal, as both processes are strictly linked.

As a next step, incorporating SECR models into Integrated Population Models in the form of spatially-explicit IPMs (SEIPMs; Chandler & Clark, 2014) can provide deeper insights into the dynamics of long-lived populations. As mentioned in previous paragraphs, models of population dynamics normally focus on modelling birth and death processes for convenience while ignoring both emigration and emigration, although these two processes can be of central relevance. Thanks to the flexibility of SECR methods, IPMs, and data integration, it could be possible to estimate all four BIDE components (birth, immigration, death, emigration) and their dynamics along time. Emigration probabilities can be obtained from SECR models as individual probabilities to permanently leave a study area (Gilroy et al., 2012; Schaub & Royle, 2014). Data on the immigration process are usually much harder to obtain by mark-recapture methods. However, immigration probabilities may be estimated by IPMs without explicit data by making use of the indirect information provided from the rest of datasets, such as count, productivity, survival, and emigration data (i.e., "hidden parameter estimation", Abadi et al., 2010). Overall, the consideration of both immigration and emigration in IPMs may help at understanding the role of local populations as net importers or exporters of individuals to neighbouring populations, that is, sink-source dynamics (Runge et al., 2006; Furrer & Passinelli, 2016). Knowledge of sink-source dynamics may allow to comprehend the mechanisms that sustain local and neighbouring populations, and therefore, can be of great relevance for the management of global populations and metapopulation systems (e.g., Hernández-Matías et al., 2013). In the last decades, robust assessments of source or sink status have been very difficult to perform due to the inherent difficulty in obtaining estimates of true survival and migration processes (Furrer & Passinelli, 2016; Heinrichs et al., 2019a). However, this may become considerably easier with SEIPMs (Paquet et al., 2020). Importantly, SEIPMs have been scarcely implemented in long-lived species thus far (Chandler & Clark, 2014). Hence, considering all their potentialities, the use of SEIPMs provides an exciting opportunity to model and understand the processes that shape the population dynamics of long-lived species at an unprecedented level of detail.

Spatially explicit IPMs also present an ideal opportunity to gain insights into the dynamics of a frequently understudied but very relevant population stage in long-lived species: floater populations. Many long-lived populations are structured into the breeding and the floating (i.e., non-breeding) fractions (Hunt, 1998; Penteriani et al., 2011). Breeding populations are those that attempt reproduction in breeding seasons, for which they may hold a breeding territory. Instead, floating populations are conformed by those individuals that, being sexually mature, still do not reproduce. There are several biological reasons and ecological scenarios that may explain the role of floaters. A common reason is a lack of breeding territories or potential mates, which often occurs in cases of habitat saturation or strong density-dependence processes (Hunt, 1998; Winker, 1998; Penteriani et al., 2011). Floaters may also be individuals who reject vacant breeding spots in wait for access to higher quality sites or mates (Kokko & Sutherland, 1998). The role of floaters in population dynamics has been understated for a long time, and most monitoring programmes still focus on breeding populations only (Penteriani et al., 2011). However, this population stage has an important role for population stability and excluding it from monitoring and modelling schemes may lead to a poor understanding of population dynamics (Lee et al., 2017; Katzenberger et a., 2021; Oppel et al., 2022). First, floaters function as a pool of individuals ready to enter the breeding population when breeders die. This mechanism is known as the buffer effect and in many cases is key to sustain stable breeding populations. In cases of high breeder mortality, the buffer effect may contribute to keeping breeder numbers constant while there are enough individuals available in the floater population (Penteriani et al., 2011). Whenever floater populations are drained, declines in breeding populations may be sudden and abrupt (Penteriani et al., 2008; Katzenberger et al., 2021). At the same time, floaters can be active participators in intraspecific competition processes for food and breeding territories. Floaters may act as intruders that engage in active disputes for mates or territories, which may end up in increased mortality or decreased productivity (Newton, 1979; Bretagnolle et al., 2008, Penteriani et al., 2011). Because of these reasons, floaters are often regarded as a double-edged sword for population regulation. Given these findings that highlight their potentially central role in long-lived population dynamics, floaters are starting to be considered in population models, such as PVAs (Katzenberger et al., 2021), and IPMs (Oppel et al., 2022). However, further precision in their study may be achieved using SEIPMs. Indeed, non-breeding birds may present large dispersal patterns until they stabilize as breeders (i.e., natal dispersal). Hence, this population stage may be one of the most affected by permanent emigration. Estimating true survival using SECR methods could be a way to understand the differential effects of mortality and emigration in this stage, which may ensure a deeper understanding of their dynamics and migratory fluxes.

Survival estimations and the reliability of Population Viability Analyses

Up until now, this introduction has presented several example in which the estimation of either apparent or true survival could lead to different model results, conclusions about population status and dynamics, or management decisions. This situation also applies to demographic population viability analyses (PVAs). Given the generally large sensitivities of population growth rates to survival, the differences between apparent and true survival could lead to considerably different population forecasts in the same population (Saether & Bakke, 2000; Lieury et al., 2016). This apparently important point of PVAs has received considerably low attention in the literature, especially when compared to other limitations like uncertainties around estimates and predictions, density dependence modelling, or life cycle accuracy (Beissinger & Westphal, 1998; Morris & Doak, 2002; Reed et al., 2002; Chaudhary & Oli, 2020). As mentioned earlier, most PVAs avoid an explicit modelling of migration processes (i.e., emigration and immigration) and only focus on birth and mortality for convenience because precise data on migratory fluxes are difficult to obtain. However, these "closed" populations with no migration processes are rare in the wild. Therefore, this assumption may lead to two potential problems in demographic PVAs. First and obvious, circumventing two of the four main BIDE processes – immigration and emigration –may lead to poor predictions of population dynamics. Second, if apparent survival is used, emigration processes are accounted for implicitly, as apparent survival is a combination of survival and emigration. However, because immigration processes are rarely included, this may lead to a disbalance in which all population processes that lead to individual loss are considered (i.e., death and emigration), but individual-gaining processes are just partially accounted (i.e., birth). Following this rationale, using apparent survival estimates in closed-population demographic PVAs may lead to considerable risks of underestimating population numbers and overestimating extinction probabilities. Instead, true survival estimates do not implicitly account for any migratory process (Gilroy et al., 2012; Schaub & Royle, 2014). Intuitively, true survival may be an adequate choice in cases where emigration and immigration cancel each other out (i.e., Emigration – Immigration = 0). In any other situation, using true survival in a closed-population model could also lead to imbalances between the true and the modelled dynamics. At the same time, using apparent survival could deliver more accurate predictions only in populations where immigration is residual or inexistent. Given the high popularity of demographic PVAs at guiding conservation action, it is essential to assess which population scenarios are more favourable for using apparent and true survival, and to determine the potential biases in viability projections incurred by any of both estimates (Himes Boor, 2014; Chaudhary & Oli, 2020).

Nevertheless, there are specific natural scenarios where migration processes are not present or residual. This may be the particular case of some island populations (e.g., Badia-Boher et al., 2019). In many terrestrial mammals and also in some bird populations on islands, the sea can act as a natural barrier that prevents dispersal. In these cases, if study areas cover the whole distribution of a species in islands, site fidelity may be complete, and the estimation of true survival is warranted. These scenarios may be ideal to test ecological hypotheses or evaluate the effect of management actions on survival with the certainty that results are not affected by emigration behaviour. In this respect, an interesting aspect of conservation science that urgently needs further research is the effectiveness of reintroductions (Armstrong & Seddon, 2007). The role of reintroductions in combating the biodiversity crisis is central. However, there is considerable scientific concern about the general low effectiveness of reintroductions (Fischer & Lindenmayer, 2000; Brichieri-Colombi & Moehrenschlager, 2016). Among the main reasons for this situation is the lack of evidence-based knowledge about the effectiveness of different management strategies in guaranteeing reintroduction success (Armstrong & Seddon, 2007). Importantly, general reviews have revealed that specific release methods in reintroductions may be associated with higher or lower reintroduction success (Wolf et al., 1996; Fischer & Lindenmayer, 2000; Brichieri-Colombi & Moehrenschlager, 2016). However, further research is needed to understand the specific scenarios in which different strategies may be more successful, so that this knowledge becomes enough precise to guide reintroduction action. In particular, an understanding of the effects of specific management strategies on population dynamics is urgently needed, so that rapid population growth and stabilization of reintroduced population can be promoted (Taylor et al., 2017). This is especially true for long-lived species, which are often the focus of reintroductions given their compromised conservation statuses (Cardoso et al., 2011). However, obtaining evidence-based knowledge can be particularly hard for these species, as the sizes of reintroduced populations are typically low, which makes it difficult to obtain datasets that are enough large for precise statistical analyses.

Study species: the Bonelli's eagle

The Bonelli's eagle (*Aquila fasciata*) is a long-lived territorial bird with delayed maturity and low breeding rates whose distribution range extends from southeast Asia through the Middle East to the western Mediterranean (del Hoyo et al., 1992; Figure 3). As other territorial raptors, Bonelli's eagle populations are structured into two population stages with significantly different behavioural patterns: territorials (breeders) and non-territorials (non-breeders). After the post-fledging dependence period and before individuals recruit to breeding territories, Bonelli's eagles pass through a transient nomadic phase typically known as the dispersal period (Real & Mañosa, 1997). At this life stage, individuals show large movements patterns and can reach areas several hundreds of kilometers away from their birth sites (Real & Mañosa, 1997, 2001; Cadahía et al., 2010). These individuals often settle temporarily in so-called dispersal areas of the species, that is, areas with large prey availabilities located away from breeding territories that attract large numbers of young non-breeders (Real & Mañosa, 1997).

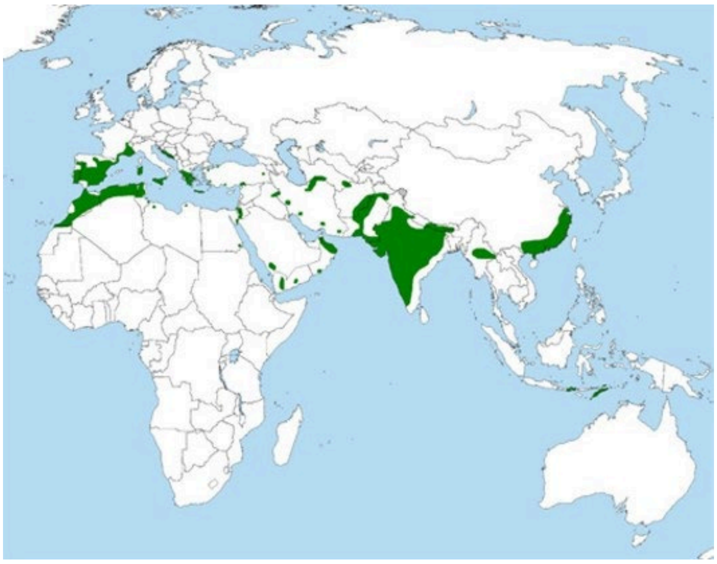

Figure 3. Global distribution of the Bonelli's eagle. Adapted from the IUCN Red List of Threatened Species (BirdLife International, 2019).

Recruitment to a breeding territory occurs at a varying age, but mostly between three and four years of age (Hernández-Matías et al., 2010). At this phase, individuals exhibit strong pair-bonding behaviour with strong fidelity to the breeding area throughout the year and throughout their lives (Bosch et al., 2010; Hernández-Matías et al., 2011a). Breeding dispersal is rare and, if present, it usually involves few kilometers. Eagles show a strong territorial behaviour with low tolerance to intraspecific intrusions. Individuals usually nest on cliffs, although nesting on trees is not uncommon in some populations (Dias, 2021). The breeding season extends from December to June. Individuals usually lay eggs between January and March. Two to three eggs are often laid, and the productivities of breeding pairs are low but variable among populations, oscillating between 0.605 and 1.422 fledglings per pair (Hernández-Matías, 2013; del Moral & Molina, 2018). Variations in plumage colour patterns allow the aging of birds between juveniles (i.e., 1 year old), immatures (2 years old), subadults (3 years old), and adults (4 years old and older). The species mainly feeds on rabbits, partridges, and pigeons, although some other occasional preys may be squirrels, other types of birds, and reptiles (Real, 1991; Moleón, 2009, 2012).

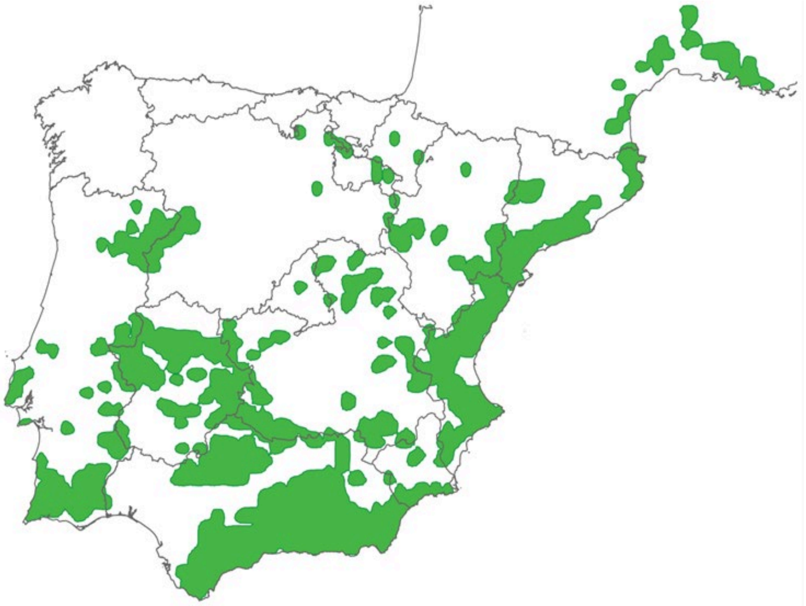

Figure 4. Bonelli's eagle distribution in continental Western Europe at fine-scale resolution.

In western Europe, the distribution of the Bonelli's eagle is generally continuous, although the range becomes relatively patchy at the western and northern edges (BirdLife International, 2019; Figure 4). The total breeding population in western Europe has been estimated at 920 to 1100 pairs, of which ca. 80% are located in the Iberian Peninsula (del Moral & Molina, 2018; BirdLife International, 2019). In the second half of the 20th century, western European populations suffered considerable declines, which led to assessments listing the species as endangered both in Spain (Real, 2004) and in Europe

(BirdLife International, 2004). In more recent times, the decreasing trends in Europe became milder, which warranted a more recent evaluation as least concern (BirdLife International, 2021).

From the 2000s onwards, local populations across western Europe have shown markedly different trends and considerable variation in key demographic parameters, such as survival and fertility, to the extent that specific populations reverted their declines and others kept declining (Carrascal & Seoane, 2009; Hernández-Matías et al., 2013, del Moral & Molina, 2018). Because of this, the continental western range of the species was defined as a sink-source system where populations in the southern half are net exporters that contribute to the stability of northern populations (Hernández-Matías et al., 2013). At present, more recent data suggest that the local dynamics of specific populations is varying again, with improved situations in some northern populations like southern France, Catalonia, and western Castilla y León, and considerable declines in others like Valencia, Aragon, and Navarra (Chevallier et al., 2015; del Moral & Molina, 2018). Such different dynamics across space are thought to be caused by variations in environmental conditions, including prey availability, mortality threats, and expansions of the range of competitive species. Electrocution and collision with power line infrastructure is currently considered the main mortality threat across populations (Hernández-Matías et al., 2015). Large retrofitting efforts of power lines have probably contributed to survival improvements at specific populations like France (Chevallier et al., 2015) and Catalonia (Hernández-Matías et al., 2020a). In addition, poisoning, drowning in human infrastructure, and direct persecution are other main causes of non-natural mortality whose intensity may be varying across space. Fecundity estimates also show considerable variations between populations with reported decreases in some, probably because of increased disturbances around nests or reductions in prey availability (Fernández et al., 1998; Hernández-Matías et al., 2013).

The Bonelli’s eagle as a study case: research opportunities from the study of two intensively monitored populations

This thesis uses available demographic and ecological data of two Bonelli’s eagle populations located in western Europe: the local population in Catalonia and the recently reintroduced population on the island of Mallorca. The Catalan population is located in the north-eastern apex of the Iberian Peninsula. The distribution of the species in Catalonia ranges from the French border in the north to the southern limits of the Ebre Delta in the south (Figure 5). The range is characterized by Mediterranean landscapes and habitats, with an average annual rainfall of 425 to 665 mm, and breeding territories situated between 30 and 780 m asl. Like other populations in western Europe, the Catalan population underwent a considerable decline in the second half of the 20th century, from ca. 85-90 breeding pairs in the 1970s to ca. 63 pairs in 2000 (Figure 5). In the beginning of the 2000s, the population stabilized at 65-70 pairs, while a sustained recovery to ca. 82 pairs occurred between the 2010s and the 2020s (del Moral & and Molina, 2018).

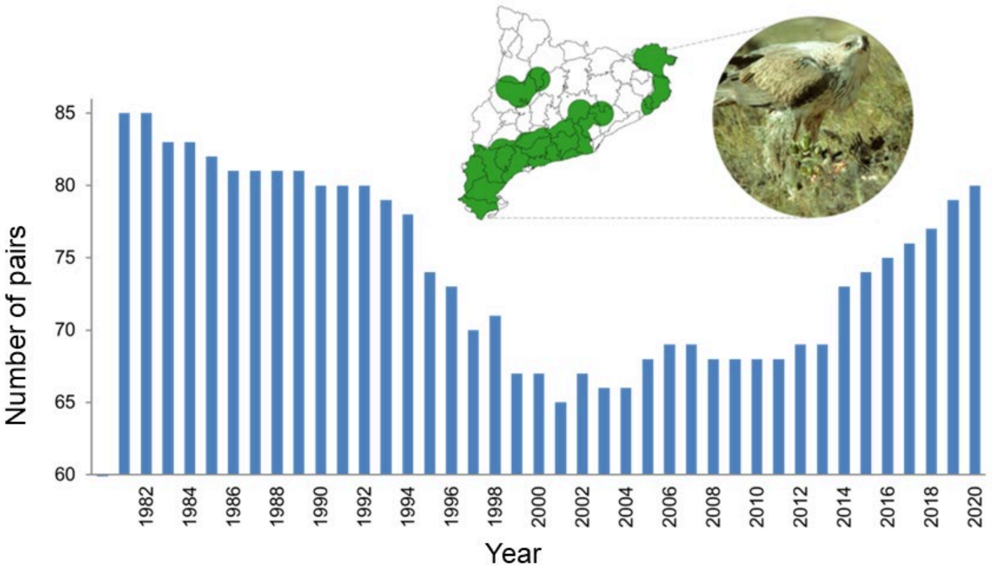

Figure 5. Distribution of the Bonelli’s eagle in Catalonia and yearly numbers of breeding pairs provided by census data(1981-2020).

The Catalan population has been intensively monitored by the Conservation Biology Team at the University of Barcelona and Catalan Government institutions for decades, which has resulted in high-quality monitoring data encompassing multiple generations of this species. Hence, this lays an exceptional opportunity to use this population as a study system in order to gain insights into the long-term population dynamics of long-lived species and their conservation. In particular, detailed surveillance data of breeding territories are available from the 1980s until present, which include 1) counts of yearly breeding pair numbers, 2) information on the number of fledglings raised per breeding pair per year, and 3) data about the yearly age composition of the breeding population and replacements of individuals in breeding pairs. In addition, intensive long-term tagging and resighting schemes were launched in two different periods during the last decades. First, 130 individuals were ringed as chicks in their nests between 1986 and 1992, and intensive efforts to recontact tagged birds were undertaken until 1999. Second, 461 additional individuals were ringed as chicks between 2008 and 2020, and field resighting efforts have lasted until present. In addition, considerable efforts by research teams, rangers, and public institutions have been devoted to recover and report dead marked individuals, especially in breeding territories and around human infrastructure, such as power lines and artificial ponds. Overall, between 1986 and 2020, 196 ringed birds were recontacted alive, of which 95 were reported as live breeders, and 103 were recovered dead.

Altogether, the availability of long-term intensive territory monitoring and mark-resighting data, together with the particularities of this study population, can make it an exceptional case of study to implement novel analytical formulations to deal with the previously described issue of permanent emigration and provide key insights about its magnitude, intrapopulation effects, and implications for the conservation of long-lived species. In this respect, apparent survival estimates of the local population in Catalonia could be considerably affected by permanent emigration. The Bonelli's eagle shows considerably large natal dispersal, and hence birds may recruit to territories that are several hundreds of kilometers away from breeding areas (Real & Mañosa 1997, 2001; Cadahía et al., 2010; Hernández-Matías et al., 2010). This natal dispersal capacity can easily overcome the limits of the Catalan study area (Hernández-Matías et al., 2010;

2013). Indeed, marked non-breeders and breeders are often seen either alive or dead in neighbouring and distant populations. In this respect, a distinctive point of this study system is that most populations in western Europe have been intensively monitored in recent decades (Hernández-Matías et al., 2013; del Moral and Molina, 2018). This is not common in most ecological studies, where the ranges of species away from study areas are rarely or not at all monitored, and hence, there is few to no information on individuals that disperse outside. Hence, the Catalan population may constitute an ideal study case to design, implement, and calibrate Bayesian spatially-explicit capture-mark-recapture methods (SECR) to estimate true survival along with true natal dispersal parameters and permanent emigration probabilities in long-lived species. By implementing SECR models to only local mark-encounter data from Catalonia, we have the opportunity to estimate true survival in a case of data limited to the study area, as is commonplace in most study designs. In addition, we could also implement SECR models to data of locally tagged birds recontacted all over the range of the species in western Europe, which should deliver precise and accurate estimates of true survival, natal dispersal, and other relevant demographic parameters (Schaub & Royle, 2014). By comparing the resulting estimates of both models to those of models that just estimate apparent survival, this study design based on real data may allow to comprehend the effectiveness of SECR methods at retrieving true estimates of demographic parameters in cases of data limitation. This knowledge may be very valuable to further understand the capabilities and constraints of these novel analytical tools for true survival and permanent emigration estimation in long-lived species.

Next, incorporating these SECR models into spatially-explicit Integrated Population Models (SEIPMs) can provide fine-scale long-term knowledge of the temporal variations of all four BIDE processes (Birth, Immigration, Death, and Immigration) along with a deep understanding of the functioning of relevant population stages in long-lived species (i.e., different age classes, and the floater and breeder stages). This may be especially relevant considering that the breeding Catalan population underwent a declining phase followed by a stabilization and a relatively rapid recovery in recent years. The availability of long-term monitoring data, from which productivity, census, and survival estimates can be obtained, can provide a deep understanding about the functioning of long-lived populations in different phases of population growth. In addition, SEIPMs may be especially useful at estimating sink-source status and dynamics. Because SEIPMs enable an explicit modelling of all BIDE processes, this facilitates a straightforward estimation of sink-source status year by year (Runge et al., 2006). The implementation of this method to the Catalan study population would help at understanding its long-term role within the global Bonelli's eagle spatially-structured range in western Europe. Importantly, this could provide valuable information about how, why, and how much sink-source status may vary in the long-term in long-lived populations, which still remains a large gap of knowledge in population dynamics (Heinrichs et al., 2016, 2019b).

The use of demographic Population Viability Analyses (PVA) is widespread in long-lived species. This is also the case of the study population in Catalonia, which has been subject to PVAs both for scientific works (Hernández-Matías et al., 2013), and technical reports (Hernández-Matías et al., 2020b). The use of SECR methods to obtain estimates of apparent and true survival in the study population lies an opportunity to quantify the magnitude of potential differences in PVA projections when using each of both estimates. This may provide an understanding of the suitability and/or potential biases associated with the use of each type of estimate. The study population in Catalonia may be an ideal study case to extract global conclusions about this topic for long-lived species. Indeed, for reliable predictions of demographic PVAs, it is essential, first, to accurately model the species life cycle, and second, to use precisely estimated stage-specific demographic parameters. In the first case, the extensive literature available about the species has favoured a detailed knowledge about its biology, ecology, and life cycle (Real & Mañosa, 1997, 2001; Cadahía et al., 2010; Hernández-Matías et al., 2010, 2011). In the second case, the long-term life-encounter datasets available may ensure a large enough sample size to obtain precise estimates of age, sex, and stage-structured survival, along with productivity.

The second population of study in this dissertation is the recently reintroduced Bonelli's eagle population on Mallorca Island. Mallorca is the biggest island of the Balearic archipelago, located in the western Mediterranean and ca. 200 km away from the Catalan coast. According to the records, the Bonelli's eagle became extinct around the 1970s in the island due to habitat loss, prey shortages, and especially direct persecution. In 2011, with the aim of re-establishing a self-sustainable population on the island, a reintroduction programme was initiated, in which 39 individuals were released until 2016. Interestingly, released individuals were of three different origins. In particular, 23 eagles were released as fledglings via the hacking method, of which 9 chicks were obtained from nests in wild populations, and 14 chicks were obtained from captive breeding programmes. The hacking method is widely used in raptor reintroductions, and consists of raising fledglings in artificial nests inside the reintroduction area and without adult conspecifics to release them as juveniles (Dzialak et al., 2006). The 16 remaining eagles were grown-up non-juveniles relocated from wild populations in continental western Europe. All individuals were tagged with PVC rings and GPS devices. By 2016, five breeding pairs had been established on the island, which had successfully raised six chicks. To date, no eagles have either been observed attempting to cross to neighbouring islands in the archipelago or to continental Europe. The exceptional conditions of this reintroduction, where alternative release strategies are simultaneously used, provides an ideal scenario to estimate demographic parameters for each strategy (i.e., survival, recruitment to the breeding population), and using populations models, evaluate the demographic contribution of each strategy to the establishment of a stable reintroduced population. In addition, since detailed information is available about the economic costs associated to each strategy, the performance of each approach can also be evaluated from a cost-effectiveness perspective. This information may provide detailed evidence-based insights about the effectiveness and cost-effectiveness of different strategies used in raptor reintroductions, thus being relevant information to guide management decisions and increase their effectiveness.

Aims and scope

In this thesis, we took advantage of the recent advances in the degree of sophistication and flexibility of population models to generate relevant knowledge for the study of population dynamics and conservation of long-lived species. Our main aim was to develop a spatially-explicit mark-recapture formulation for the estimation of permanent emigration and true survival to 1) evaluate the differences between apparent and true survival and their different magnitudes in different population stages of long-lived species, 2) implement spatially-explicit integrated population models to provide more complete descriptions of population dynamics, including the often overlooked dynamics of floater populations, migration processes, and sink-source status, and 3) evaluate the frequently ignored effects of the use of true and apparent survival on PVA projections and reliability and discuss the implications of this issue for wildlife management. A secondary aim of this thesis was to contribute to increase the effectiveness of reintroductions by generating evidence-based knowledge about the effectiveness of different strategies used in raptor reintroductions. To address these objectives, we structured the thesis in four different chapters, which are described hereunder.

In **Chapter 1**, we evaluated the contribution to reintroduction success and the cost-effectiveness of three different release strategies in raptor reintroductions: first, the release of eagles from captive breeding as fledglings using the hacking method; second, the release of eagles extracted from wild nests as chicks using again the hacking method; and third, the release of wild-reared, non-juvenile eagles captured in wild populations and relocated to the reintroduction area. As a study case, we used the recent Bonelli's eagle reintroduction in the island of Mallorca (2011-2016), where the three release strategies were simultaneously used. To evaluate contribution to reintroduction success, we estimated age-specific survival and recruitment parameters and incorporated them into individual-based demographic population viability analyses (PVA), and we compared the predictions of the models under the demographic estimates obtained by each release method. Cost-effectiveness was evaluated by incorporating cost estimations of each method into the PVAs and comparing results under different budgets.

In **Chapter 2**, we developed a multistate extension of Bayesian spatially explicit capture-mark-recapture models (SECR) to differentiate true survival, recruitment, and natal dispersal parameters from permanent emigration in long-lived species. To do so, we assembled a hierarchical model that consisted of two units: a multistate capture-mark-recapture submodel to estimate age, sex, and stage-specific survival, recruitment, recapture, and recovery probabilities; and a spatial model to define the distribution of the species in western Europe and estimate natal dispersal and permanent emigration probabilities. The key step of this extension is to link the multistate and the spatial submodel appropriately so that natal dispersal, true survival, and detection probabilities across space could be jointly estimated. Because encounter data of individuals marked in Catalonia and dispersed to other populations in western Europe were available, we could evaluate the ability of SECR models to retrieve true survival estimates when data of the whole range were available, compared to cases where the available data are restricted to the study area.

In **Chapter 3**, we merged the SECR framework developed at chapter 2 with an Integrated Population Model (IPM) to study the long-term dynamics of the Bonelli's eagle population in Catalonia (1986-2020) and generate general knowledge for long-lived species demography. To do so, we took advantage of the long-term territory surveillance, productivity, and tagging-resighting schemes available from the study population. The combination of SECR models and IPMs allowed for the modelling of the dynamics of different population stages: the breeding and the floating population, the numbers of emigrants and immigrants, and variations in sink-source status along time. As the 35 years of modelling encompass a decline (1986-1999), stabilization (2000-2010) and recovery of the Catalan population (2011-2020), results could provide a mechanistic understanding on the functioning of different population fractions and their contribution to population dynamics in different stages of population growth in long-lived species.

In **Chapter 4**, we evaluated the differences in the predictions of demographic PVAs when using either apparent or true survival estimates in long-lived species. In addition, we evaluated how the explicit modelling of migration processes (i.e., emigration and immigration) could modify the accuracy of PVAs based on apparent and true survival. To do so, we developed individual-based demographic PVAs adapted to the life cycle of the

Bonelli’s eagle following the extensive knowledge on the species biology and population dynamics. The estimates of true and apparent survival used in the PVAs were those estimated in Chapter 2. Based on the results of our predictions, we carefully evaluated the appropriateness of each type of survival estimate in different population scenarios and discussed potential ways to estimate and incorporate migration processes in demographic PVAs.

Supervisor's report

Joan Real Ortí and Antonio Hernández-Matías, co-directors of the doctoral thesis titled "Population Models: Flexibility, Advances and Applications to Wildlife Conservation. The Bonelli's Eagle as a Study Case" authored by Jaume Adrià Badia-Boher, hereby certify that the candidate has carried out the research described in this thesis. The thesis is composed of four different scientific works, of which two are already published in international scientific journals listed in the Science Citation Index (SCI). Hereunder, we list these two articles, along with the contribution of the candidate to each of them, and the impact factor of each journal. In addition, we certify that no coauthors of these articles or other works presented in this doctoral thesis have used implicitly or explicitly these works as part of other theses.

Chapter 1. Badia-Boher, J. A., Hernández-Matías, A., Viada, C., & Real, J. (2022). Raptor reintroductions: Cost-effective alternatives to captive breeding. *Animal Conservation*, 25(2), 170-181. https://doi.org/10.1111/acv.12729

Contribution of the candidate: Design and development of analytical methods, interpretation of the results, leading of manuscript writing.

About the journal: *Animal Conservation* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 4.377 (2021). The Impact Factor of the journal was listed as number 12 out of 65 in the field of biodiversity conservation (first quartile), and as number 48 out of 173 in ecology (second quartile).

Chapter 2. Badia-Boher, J. A., Real, J., Riera, J. L., Bartumeus, F., Parés, F., Bas, J. M., & Hernández-Matías, A. (2023). Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses. *Scientific Reports*, 13, 6970. https://doi.org/10.1038/s41598-023-32866-0

Contribution of the candidate: Design and development of analytical methods, data cleaning and wrangling, interpretation of the results, leading of manuscript writing.

About the journal: *Scientific Reports* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 4.997 (2021). The Impact Factor of the journal was listed as number 19 out of 74 in the field of multidisciplinary sciencies (second quartile).
Barcelona, 24th May 2023

Prof. Dr. Joan Real Ortí (Thesis co-director and mentor)
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Facultat de Biologia

Hernández

Prof. Dr. Antonio Hernández-Matías (Thesis co-director)
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Facultat de Biologia

CHAPTER 1

Raptor reintroductions: Cost-effective alternatives to captive breeding

Photograph courtesy of Jaume Elies

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Raptor reintroductions: Cost-effective alternatives to captive breeding

Jaume Adrià Badia-Boher[1], Antonio Hernández-Matías[1], Carlota Viada[2] & Joan Real[1]

1 Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia I Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Catalonia, Spain
2 LIFE Bonelli, Govern de les Illes Balears-COFIB, Palma, Spain

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Correspondence
Jaume Adrià Badia-Boher, Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia I Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Catalonia, Spain.
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Abstract

Reintroductions are becoming a popular tool to prevent extinctions, although their overall success rate is low. Assessing the efficiency and cost-effectiveness of different reintroduction strategies may help identify and promote efficient practices. Captive-breeding is widely used in animal reintroductions, although concerns have been raised about relatively high failure rates and economic costs. Here, we compared the effectiveness of two simultaneously used strategies in the reintroduction of the Bonelli's eagle on the island of Mallorca: The release of captive-bred chicks and wild-reared, translocated non-juveniles. To do so, we estimated the main vital rates for individuals released by both strategies and used these to perform population simulations to assess their overall performances. The use of wild-reared non-juveniles showed a trend with higher numbers of breeding pairs 10 years after the end of releases (14.75 pairs, 95% CI 4–25 vs. 11.21 pairs, 95% CI 2–24) and was the only strategy that prevented extinction in the long term. Following that, based on cost estimations of every strategy and different reintroduction budgets, we assessed the cost-effectiveness of releasing wild-reared non-juveniles compared with two captive-breeding alternatives: Releasing chicks either originally from breeding programmes or extracted from nests in natural populations. Again, releasing wild-reared non-juveniles was the only strategy that prevented long-term extinction in all economic scenarios (i.e. low-budget scenario 21.49 pairs, 95% CI 2–25). The use of chicks sourced from captive-breeding programmes did not guarantee long-term persistence even in high-budget scenarios (14.50 pairs, 95% CI 0–25). Releasing wild-reared non-juveniles boosts early recruitment to the breeding population and early reproduction, which can be key for reintroduction success. However, in some scenarios, post-release effects can be stronger in wild-reared individuals, especially because of high translocation stress and post-release dispersal. Hence, we recommend undertaking careful evaluation of the pros and cons of every strategy and embracing adaptive management to choose best strategies.

Introduction

Animal reintroductions are becoming a widespread tool to combat the current extinction crisis. However, the outcomes of such actions are not always successful, with global failure rates estimated between 33% and 89% (Beck *et al*., 1994; Wolf *et al*., 1996; Fischer & Lindenmayer, 2000; Griffiths & Pavajeau, 2008; Brichieri-Colombi & Moehrenschlager, 2016). Economic constraints for conservation are a critical reason to increase the effectiveness of reintroductions (Naidoo *et al*., 2006). Hence, it is important to identify and promote cost-effective strategies to allocate economic and human resources efficiently. However, although the number of studies reporting the costs of reintroduction attempts is increasing, there is still little evidence from which to extract robust cost-effectiveness conclusions (Fischer & Lindenmayer, 2000; Naidoo *et al*., 2006; Wakamiya & Roy, 2009; Wilson *et al*., 2009; Canessa *et al*., 2014; Morandini & Ferrer, 2017; Ferrer *et al*., 2018; Pienkowski *et al*., 2021). In this context, population modelling can be a helpful tool, as it allows for analyses and comparisons between alternative strategies before they are implemented.

Improving knowledge about the factors that affect the success of reintroductions is essential in pinpointing effective strategies and providing evidence-based guidance to managers. As available research shows, potential drivers of reintroduction outcomes include species-specific behavioural and life-history traits (Wolf *et al*., 1996; Reed, 1999), the age of released individuals (Le Gouar *et al*., 2008), habitat quality (White *et al*., 2012), presence or absence of potential predators (Sheean *et al*., 2012), numbers of individuals released (Fischer & Lindenmayer, 2000) and the release methods and the origin of the released individuals (i.e. captive-born vs. wild-born) (Hardman & Moro, 2006; Buner & Schaub, 2008; Rummel *et al*., 2016). A common challenge of reintroductions is that individuals usually show higher chances of mortality during the first months following release (Tavecchia *et al*., 2009; Armstrong *et al*., 2017). This phenomenon is known as the 'cost of release' or 'post-release effect' and is usually caused by stresses associated with the translocation process or the adaptation to the area of release (Tavecchia *et al*., 2009; Dickens *et al*., 2010; Armstrong *et al*., 2017).

The use of captive-born individuals from breeding programmes is widespread in reintroductions (Araki *et al*., 2007). This strategy usually provides large stocks of individuals available for release, which can be key for reintroduction success (Fischer & Lindenmayer, 2000). However, such programmes involve high economic and technical costs associated with animal husbandry (Snyder *et al*., 1996; Ferrer *et al*., 2018). Captive-bred individuals also usually show lower survival probabilities than their wild counterparts, possibly because they lack predator avoidance and/or foraging abilities (Buner & Schaub, 2008; Tavecchia *et al*., 2009). On the other hand, the use of wild-reared individuals is generally associated with higher reintroduction success according to practitioner surveys and reviews (Fischer & Lindenmayer, 2000; Jule *et al*., 2008; Rummel *et al*., 2016).

Raptors are among the most threatened taxa worldwide and are common targets of reintroduction projects (McClure *et al*., 2017). The main reintroduction strategy for raptors is the hacking method, which consists of captive breeding of fledglings in artificial nests – without adult conspecifics and preventing contact with humans – then releasing them as juveniles (Dzialak *et al*., 2006; Oro *et al*., 2011). Many hacking schemes rely on captive breeding programmes for stocks of birds to release, which usually substantially raises the costs of reintroductions. A hacking alternative that avoids implementing breeding programmes, and consequently lowers the economic demands associated with the reintroduction, is the use of chicks extracted from wild nests in natural populations (Ferrer *et al*., 2018). Importantly, the hacking method implies releasing juveniles, which involves no reproduction until birds reach sexual maturity. Instead, early reproduction of released birds can greatly contribute to the success of reintroductions (Morandini *et al*., 2019). This is usually due to three causes: First, early reproduction implies higher chances of adding new individuals to the population before released birds are removed by mortality in later years; second, these new individuals born in the reintroduction area frequently show higher survival prospects than released conspecifics (Brown *et al*., 2006) and third, breeding individuals may have reduced probabilities of mortality compared with non-breeders, especially in long-lived territorial species (Morandini *et al*., 2019). An effective measure to promote early reproduction is the release of non-juvenile individuals, especially sexually mature ones (Sarrazin & Legendre, 2000; Robert *et al*., 2002; Evans *et al*., 2009). However, for strategies relying on captive breeding, this is usually economically demanding, as it means assuming the costs of bird care for years before release (Martínez-Abraín *et al*., 2011). Instead, the translocation of wild, non-juvenile individuals from natural populations to reintroduction areas could present a cost-effective alternative to boost early reproduction.

Here, using reintroduction simulations, we sought to evaluate the cost-effectiveness of three reintroduction strategies: Hacking based on captive breeding (hereafter 'CaptHack'), hacking based on chicks extracted from wild nests in natural populations ('NestHack') and the translocation of wild, non-juvenile birds from natural populations recovered from rehabilitation centres ('WildTrans'). We compare the contribution with reintroduction success of the two hacking methods and WildTrans, and quantify the costs of all three methods and compare their contribution to long-term population viability under different economic budgets. Our study focuses on the reintroduction of the Bonelli's eagle *Aquila fasciata* in the island of Mallorca, where all three strategies were used simultaneously. Thanks to the detailed monitoring of released birds in the area (2011–2016) and the comprehensive knowledge of the life history of the species in Europe (e.g. Hernández-Matías *et al*., 2013), we could estimate the key demographic parameters for every reintroduction strategy and develop individual-based population models to simulate reintroductions by all methods. We expect our results to provide important evidence-based insights for practitioners on long-lived species reintroductions.

Materials and methods

Study species and area

The Bonelli's eagle (*A. fasciata*) is a long-lived territorial raptor whose range extends from south-east Asia to the western Mediterranean. It is assessed globally as Least Concern, but as Near Threatened in Europe and Endangered in Spain (Birdlife International, 2015, 2019), where the species underwent severe declines and local extinctions in the last decades. Here, we focus on Mallorca Island, where the species died off around the 1970s due to habitat loss, prey shortages and especially direct persecution. A reintroduction programme was launched in 2011 with the aim of re-establishing a self-sustainable population in the area. A total of 39 individuals were released between 2011 and 2016: 9 chicks via NestHack, 14 chicks via CaptHack and 16 non-juvenile individuals (>1 year old) via WildTrans. All released individuals were tagged with PVC rings and GPS devices. By 2016, five breeding pairs had established in the area, which had successfully raised six chicks.

Model definition and main structure

To assess the effectiveness of CaptHack, NestHack and WildTrans strategies, we designed individual-based models that simulated the life cycle of the species in a population structured by sex, age and territorial status and limited by density-dependence. We estimated vital rates (i.e. survival, recruitment to the breeding population and productivity) from our own data where possible, but given the small sample size of our reintroduced population, we used estimates from conspecific Iberian populations when specific values were not estimable (Hernández-Matías *et al*., 2013) (see Methods: Estimation of vital rates). We considered survival and recruitment to the breeding population (hereafter, 'recruitment') to vary with age and release strategy, assuming that hacking birds of both origins and wild birds born in the reintroduction area would share the same estimates. Productivity was assumed to vary with age but not among release strategies. We modelled the different reintroduction scenarios by simulating eagle releases for the first 10 years in overall 50-year simulations with a starting population size of 0 individuals. We accounted for environmental (adult survival and productivity) and demographic stochasticity (all vital rates). Detailed model specifications are provided at Methods: Model settings. Based on these features, we assessed the performance of the evaluated reintroduction strategies using two sets of analyses: First, we assumed the same number of individuals released under hacking and WildTrans strategies to assess their performance in terms of release effort irrespective of their economic cost and second, we assessed the cost-effectiveness of each strategy.

Hacking versus WildTrans effects on reintroduction success

We simulated two different reintroduction scenarios: (1) Releasing only fledglings of hacking origin and (2) releasing only WildTrans individuals. For each of these two scenarios, we simulated the release of 6.5 eagles on average per year (SD = 1), following average numbers of observed releases.

Cost-effectiveness of CaptHack, NestHack and WildTrans

We simulated three different scenarios that consist in the release of (1) CaptHack, (2) NestHack and (3) WildTrans individuals. Each scenario was simulated under three budgets, namely, 15000 €/year (low), 30000 €/year (medium) and 50000 €/year (high). The budgets were chosen after discussion about realistic low-budget, medium-budget and high-budget incomes with managers involved in the reintroduction. In every scenario, we determined the yearly number of released eagles by dividing the corresponding budget by the individual economic cost of every eagle (Table 1). To calculate such costs, we considered the expenses associated with personnel and bird feeding associated with every released strategy. We did not include costs related to infrastructure acquisition or maintenance and journeys of monitoring or chick removal because these expenses were external to our reintroduction programme. See Data S1: Economic Estimations and Figure S1 for further details. Cost estimates amounted to 11141.6, 5061.6 and 2338.9 €/eagle for CaptHack, NestHack and WildTrans birds, respectively. Taking the resulting numbers as means (SD = 0.5), we simulated different numbers of released eagles for every strategy, budget and simulation year using a normal distribution. The scenarios showing better performance under identical budget caps were considered most cost-effective.

Estimation of vital rates

Survival and recruitment

We developed multievent capture–mark–recapture (CMR) models (Pradel, 2005; Hernández-Matías *et al*., 2015) to estimate the probabilities of recruitment and survival from 2011 to 2016. The CMR framework allows for accounting of heterogeneity in survival and resighting probabilities between individuals classified in different states, as well as for uncertainty about the states of the individuals. Our analysis considered data on live individuals and mortality events to increase our estimates' precision (Lebreton *et al*., 1999). Because our sample size was small, increasing model complexity would lead to imprecise or inestimable parameters. Hence, we split our dataset for two different analyses: One for hacking and wild birds born in the reintroduction area (n = 29 individuals: 23 hacking and 6 wild-born) and another for WildTrans eagles (n = 16 individuals). Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). We built capture–recapture histories using quarterly intervals, and the resulting estimates were raised to the power of 4 to obtain annual probabilities. The corresponding variance was estimated using the Delta Method (Powell, 2007). We followed a stepwise model selection procedure, in which we tested different age structures parameter by parameter and used those that minimized AICc in following steps (Burnham & Anderson, 2002). In addition, because of the small sample sizes of our datasets, which can lead to

Table 1 Mean number of yearly released individuals by each reintroduction method and budget scenario

	Budget		
	15000 €/year	30000 €/year	50000 €/year
Reintroduction method			
Wild, non-juvenile Translocation (WildTrans)	6.4	12.83	21.37
Nest-removed hacking (WildHack)	2.96	5.93	9.88
Captive-breeding hacking (CaptHack)	1.35	2.69	4.49

considerable effects of demographic stochasticity, we considered the statistical plausibility of the model (i.e. presence/absence of parameter estimability issues), and the biological realism of model structure and parameter estimates, based on the extensive knowledge available on the demographic features of close-by continental populations (Hernández-Matías *et al*., 2013). The models were built and run under software E-SURGE (Choquet *et al*., 2009a), and goodness-of-fit tests were implemented with U-CARE v2.2.2 (Choquet *et al*., 2009b).

Analysis for hacking and wild eagles born in the reintroduction area

The JMV goodness-of-fit test showed no deviation from assumptions ($X^2 = 0.985$, df = 7, $P = 0.995$). We built a global transition matrix considering GPS tag failure, recruitment and survival probabilities. We first selected the GPS failure and recruitment structures that minimized AICc, and then we tested six survival structures related to the age and territorial status of the eagles (Table 2). Further details are provided in Data S1: Multievent Definition and Selection.

Analysis of wild, non-juvenile, translocated eagles

The JMV goodness-of-fit test showed an adequate fit to the data ($X^2 = 1.87$, df = 8, $P = 0.985$). We defined a simpler model to avoid parameter estimability problems due to the small sample size of this dataset ($n = 16$ individuals). Thus, we did not account for GPS tag failure, but because all individuals of this type had active, working GPS devices throughout the course of the study, we believe that this decision does not violate the tag retention assumption of mark–recapture models. Starting from a general model with four age classes for recruitment and survival, we first selected the recruitment structure that minimized AICc and then tested four different survival structures according to the number of years since release and territorial status of individuals (Table 3). See further details in Data S1: Multievent Definition and Selection.

Table 2 Model selection for the survival parameter in the multievent analysis including hacking and wild birds born in the reintroduction area

Survival structure	No. parameters	Deviance	AICc
A1+A2+(A34*Recruitment status)	13	228.84	256.79
A1+A23+A4	**12**	**235.72**	**261.38**
A1+A2+A34	12	236.96	262.62
Recruitment status	12	237.06	262.72
A1+(A234*Recruitment status)	13	235.28	263.22
A1+A2+A3+A4	13	235.62	263.56

Survival model selection was performed after modelling GPS tag loss and recruitment and selecting the structures that minimized AIC for these parameters. Values 'A1', 'A2', 'A3' and 'A4' stand for the ages 1, 2, 3 and 4 and older in years, respectively. 'Recruitment status' refers to whether or not the individual has joined the breeding population. The selected model is indicated in bold.

Table 3 Model selection for the survival parameter in the multievent analysis for wild non-juvenile translocated eagles

Survival structure	No. parameters	Deviance	AICc
A1+A234	6	86.63	99.88
A1+A2+A34	**7**	**84.78**	**100.47**
A1+A2+A3+A4	8	84.78	102.99
Recruitment status	6	89.34	102.59

Survival model selection was performed after modelling recruitment and selecting the structure that minimized AIC for that parameter. Values 'A1', 'A2', 'A3' and 'A4' stand for number of years since the release of the individual in the reintroduction area: 1, 2, 3 and 4 or more, respectively. 'Recruitment status' refers to whether or not the individual has joined the breeding population. The selected model is indicated in bold.

Adult productivity

Because few data on productivity were available, we estimated productivities for individuals aged 4 and older (hereafter, 'adult productivity') based on reproduction attempts of all territorial pairs, independently of their ages, and considering reproduction events from the same pairs in different years as independent observations. Because productivity is a demographic parameter with a relatively low impact on population viability (Saether & Bakke, 2000), we believe that this did not significantly affect our results.

Use of estimates from conspecific populations

We used estimates from Iberian populations (Hernández-Matías *et al*., 2013) in cases where the data from the study population were insufficient to obtain reliable estimates. In particular, survival was not estimable for individuals aged four and older of any method, as well as recruitment of all individuals aged three and older, because of the high numbers of surviving individuals at these ages. In these cases (i.e. hacking, WildTrans and wild individuals born in the reintroduction area), we used averaged values from all 12 monitored populations in Hernández-Matías *et al*. (2013). In addition, because survival was not estimable for 3-year-old WildTrans eagles, we used the estimate obtained from the analysis of hacking and wild individuals born in the reintroduction area. Productivity values of eagles younger than 4 years old were assumed from the population in Catalonia (NE Spain) (Hernández-Matías *et al*., 2013). Temporal variances to model environmental stochasticity of adult survival and productivity were also calculated as averages of continental populations (Hernández-Matías *et al*., 2013).

Model settings

Our individual-based model followed a post-breeding census. We simulated fine-scale life-cycle processes stepwise in 1-year steps in this order: (1) Survival and mortality, (2) aging, (3) recruitment to the breeding population, (4) territory acquisition, (5) mating, (6) breeding and (7) release of reintroduced individuals (Figure S2). At the beginning of every year, we established new adult survival and productivity values following a beta distribution with the temporal variance of each parameter to simulate environmental stochasticity (Morris & Doak, 2002). Senescence was incorporated by reducing survival probabilities to 50% in individuals aged 20 years and older (Chantepie *et al*., 2016). Territory acquisition and mating are simulated conditional on the availability of both recruited males and females. The model prioritizes the occupation of vacant spots in occupied territories instead of the occupation of new territories. Individuals of higher age were considered more competitive. Therefore, in cases where territory availability is limited, older individuals have priority to enter territories. In the release process, for wild, non-juvenile, translocated eagles, we assigned random ages at release to every individual based on the observed age ratios of released birds in the study reintroduction (i.e. 1/3, 1/6, 1/6 and 1/3 for 2-, 3-, 4-year-olds and adults, respectively). Density dependence was incorporated by considering a ceiling of 25 territories in Mallorca (i.e. 25 breeding pairs), based on species distribution analysis (Viada, C., unpublished data).

Each reintroduction scenario was run for 1000 replicates. Reintroduction success for each strategy was assessed through the expected number of breeding pairs as the mean and the corresponding 95% interpercentile range between 2.5 and 97.5 percentiles (hereafter referred to as the percentile 95% confidence interval, 95% CI) of all the replicates at simulation years 20 and 50. We considered that a scenario prevented long-term extinction when 95% CI did not expand to 0 at year 50. In addition, to strengthen the value of our results, we performed an analysis evaluating parametric uncertainty in main vital rates (see Data S1: Simulations with parametric uncertainty; Figures S3 and S4). All simulations were performed using R(3.6.2) (R Core Team, 2020) and package PopBio (Stubben & Milligan, 2007).

Results

Estimation of vital rates

For hacking and wild eagles born in the reintroduction area, the best-ranked model by AICc showed parameter estimability issues; therefore, we selected the second model in the rank, whose estimates best matched the available demographic knowledge on the species (Table 2) (Hernández-Matías *et al*., 2013). In this model, yearly probabilities of survival and recruitment to the breeding population for hacking and wild eagles born in the reintroduction area increased with age. For WildTrans birds, because the best model in the AICc rank provided biologically unrealistic survival estimates, we selected the second model in the rank (Table 3). The selected model showed increasing survival probabilities depending on time since release and constant recruitment probabilities. All 3-month and annual demographic estimates are shown in Table 4. Adult productivity was estimated at 1.2 (SD = 0.74) chicks per pair and breeding attempt, which fits the range of known values of conspecific populations (0.63–1.42, Hernández-Matías *et al*., 2013). Estimates from conspecific continental populations used for modelling are also shown at Table 5.

Population viability analyses

Hacking versus WildTrans effects on reintroduction success

The number of breeding pairs obtained at year 50 for WildTrans was moderately higher (22.24, 95% CI 4–25 breeding pairs) than that for hacking releases (19.90, 95% CI 0–25; Fig. 1). The WildTrans scenario was the only one that prevented long-term extinction.

Cost-effectiveness of CaptHack, NestHack and WildTrans under different economic budgets

The release of WildTrans eagles provides considerably higher numbers of pairs than any hacking strategy under equal economic conditions (Table 6, Fig. 2). Using NestHack individuals showed a better performance than using CaptHack birds. Interestingly, the number of pairs in year 50 using the WildTrans method under the cheapest scenario (i.e. 15000€/year) was remarkably higher than the one for CaptHack under

Table 4 Parameter estimates obtained in the multievent analyses of hacking and wild birds born in the reintroduction area and WildTrans birds

Release method	Parameter	3-month estimate	Annual estimate
Hacking + wild born in reintroduction area	First-year survival	0.854 (0.035)	0.533 (0.087)
	Second-year survival	0.931 (0.033)	0.753 (0.101)
	Third-year survival	0.931 (0.033)	0.753 (0.101)
	First-year recruitment	0.073 (0.027)	0.262 (0.061)
	Second-year recruitment	0.111 (0.060)	0.376 (0.138)
WildTrans	First-year survival	0.829 (0.064)	0.471 (0.145)
	Second-year survival	0.923 (0.074)	0.726 (0.233)
	Third-year survival	0.931 (0.033)[a]	0.753 (0.101)[a]
	First-year recruitment	0.167 (0.068)	0.518 (0.136)
	Second-year recruitment	0.167 (0.068)	0.518 (0.136)

Estimates are presented with standard deviation (SD) inside parentheses. Standard deviation in annual estimates was calculated using the Delta Method.

[a] Third-year survival for WildTrans birds was picked from the analyses of hacking and wild born individuals born in the reintroduction area.

Table 5 Parameter estimates used in the population simulations obtained from sources different from our multievent analyses

Parameter	Estimate + (temp. var.)	Source
Fourth-year survival	0.8436	Hernández-Matías *et al.* (2013)
Adult survival	0.9042 (0.002)	Hernández-Matías *et al.* (2013)
>20-year survival	0.500	Assumed (senescence)
Third-year recruitment	0.680	Hernández-Matías *et al.* (2013)
Fourth-year recruitment	0.934	Hernández-Matías *et al.* (2013)
Adult recruitment	1	Hernández-Matías *et al.* (2013)
Second-year productivity	0.286	Hernández-Matías *et al.* (2013)
Third-year productivity	0.400	Hernández-Matías *et al.* (2013)
≥Fourth-year productivity	1.2 (0.328)	Own calculation

Estimates are presented with temporal variation (temp. var.) inside parentheses in those parameters where we simulated environmental stochasticity.

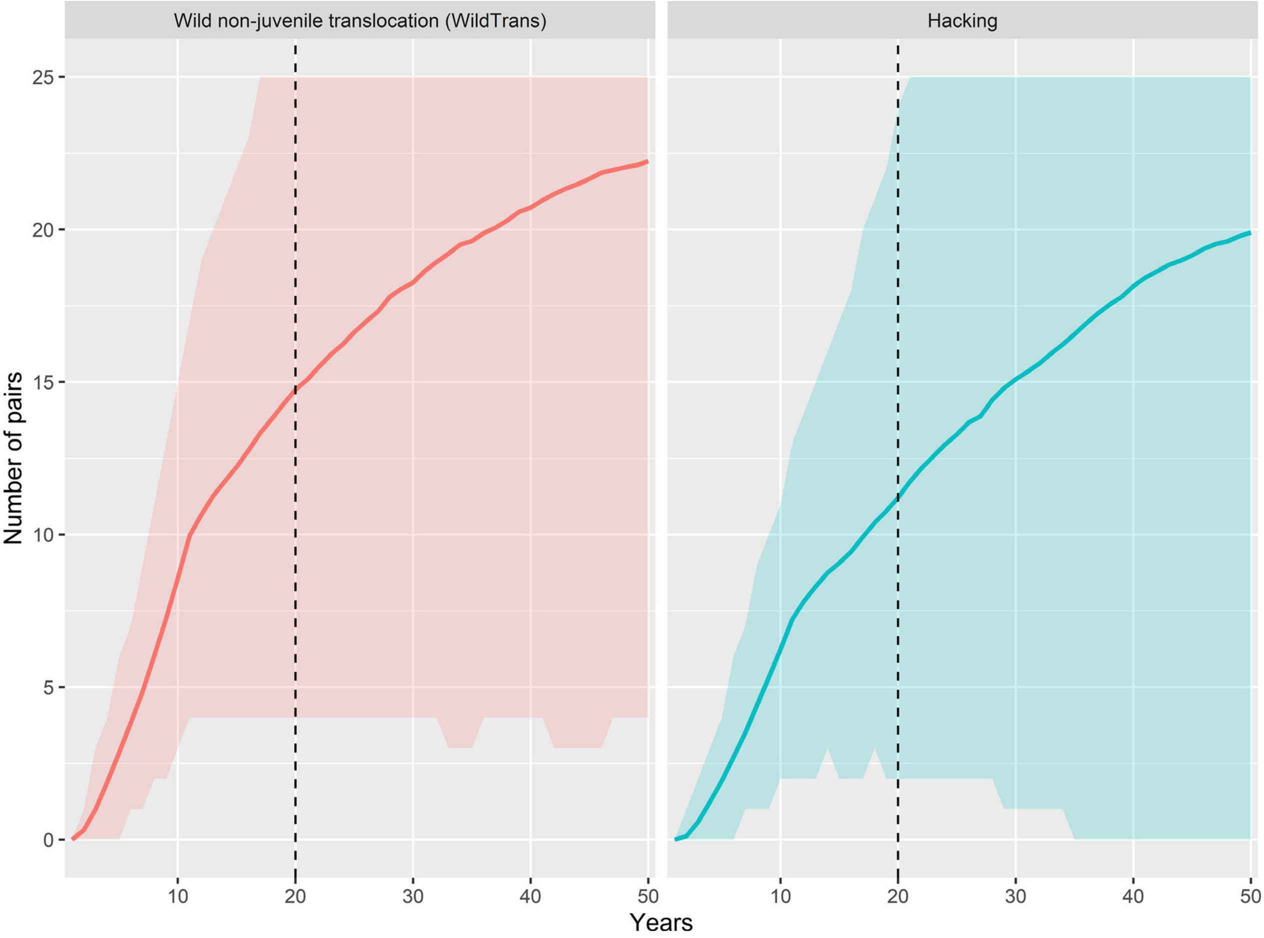

Figure 1 Comparison of the effects of hacking and WildTrans reintroductions on long-term population viability. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year, and shaded areas indicate 95% confidence intervals.

the most expensive scenario (i.e. 50.000€/year) (21.49 pairs, 95% CI 2–25 and 14.50, 95% CI 0–25, respectively). In fact, 95% CIs for the CaptHack strategy expand to 0 in all scenarios, which shows that the event of an extinction, and therefore reintroduction failure, cannot be discounted in any case.

Discussion

Assessing the cost-effectiveness of different conservation measures is essential to identify optimal strategies in modern conservation practice. Here, we used population analyses to

Table 6 Average numbers of breeding pairs under different budget scenarios and reintroduction methods for years 20 and 50 on reintroduction simulations. 95% CIs are shown in parentheses

	Budget					
	15000 €/year		30000 €/year		50000 €/year	
Reintroduction method						
Simulation year	Year 20	Year 50	Year 20	Year 50	Year 20	Year 50
WildTrans	14.081 (4–25)	21.49 (2–25)	24.23 (17–25)	24.87 (25–25)	24.97 (25–25)	24.98 (25–25)
NestHack	3.70 (0–11)	8.19 (0–25)	9.77 (2–21)	18.29 (0–25)	17.86 (6–25)	23.75 (9–25)
CaptHack	1.18 (0–6)	2.43 (0–21)	3.39 (0–10)	7.58 (0–25)	6.89 (0–16)	14.50 (0–25)

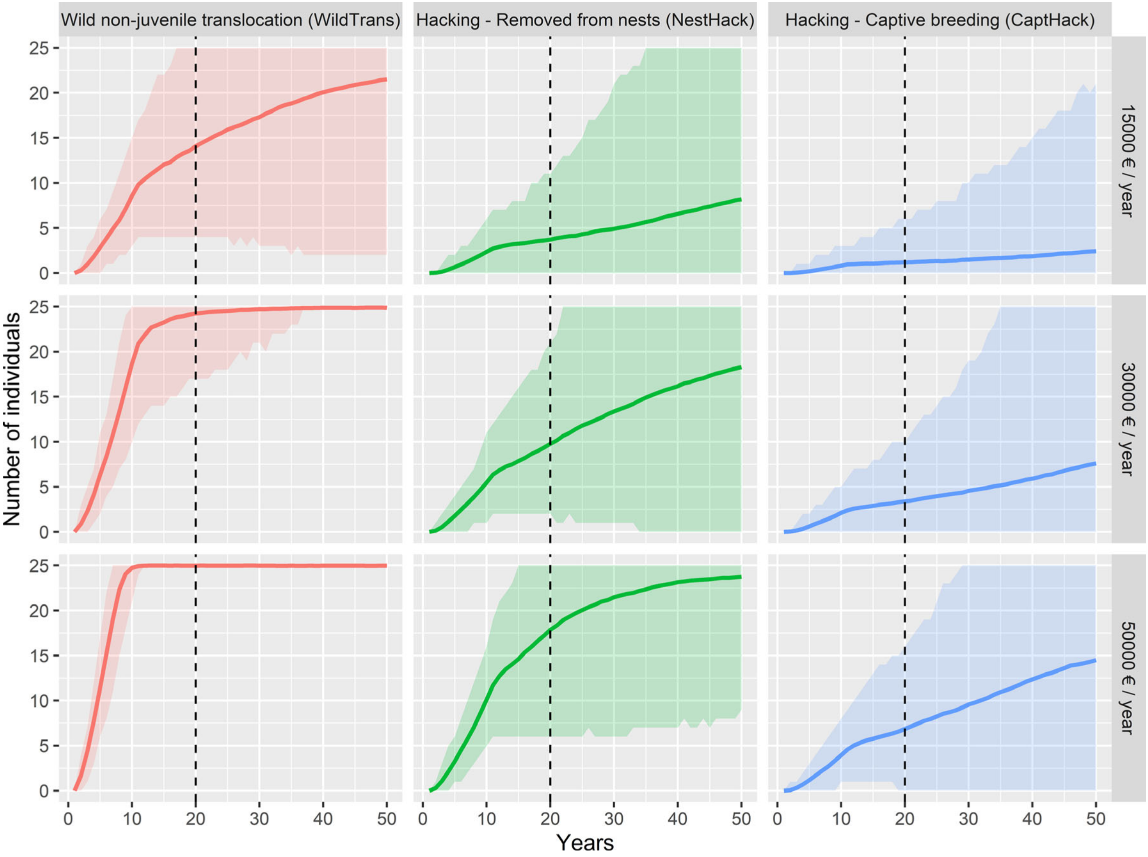

Figure 2 Cost-effectiveness comparison of the effects of WildTrans, NestHack and CaptHack reintroductions on long-term population viability under different budget scenarios. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year, and shaded areas indicate 95% confidence intervals.

compare the success and cost-effectiveness outcomes of three alternative release strategies used in a reintroduction scheme for the Bonelli's eagle on Mallorca island. Our results strongly support that the translocation of wild, non-juvenile individuals (WildTrans) is the most cost-effective strategy to establish a viable reintroduced population in our case study. Two main reasons may explain this finding. First, releasing birds older than fledglings increases the chances of forming breeding pairs – and successful reproduction – in a shorter period. Second, releasing wild, non-juvenile individuals is notably cheaper than any hacking strategy, as these methods require the implementation of captive breeding and/or bird care for longer periods. Our findings can be meaningful for other long-lived species reintroduction schemes. In addition, we highlight how including cost-effectiveness criteria in population analyses can improve the allocation of resources and the global results of wildlife reintroductions and reinforcements.

Captive breeding and hacking are widely used techniques in reintroduction programmes, despite their high economic costs and the scientific concerns about the relatively lower success rates of reintroductions when captive-reared animals are used (Fischer & Lindenmayer, 2000; Mathews *et al.*, 2005; Jule *et al.*, 2008; Rummel *et al.*, 2016). In our results, WildTrans was the only method that prevented long-term population extinction in the smallest and medium-budget scenarios (15.000 and 30.000 €/year), whereas within the highest budget (50.000 €/year), CaptHack was the only method that could not safely avoid extinction. As predicted, recruitment probabilities were considerably higher for WildTrans eagles than for hacking-released conspecifics, to the extent that half of the WildTrans birds joined the pool of potential breeders each year during the first 2 years following release. As such, shortening the time until reproduction of released birds accelerates a shift towards a population largely composed of wild individuals born in the target area, which can contribute greatly to reintroduction success (Evans *et al.*; 2009; Morandini *et al.*, 2019). As shown by Sarrazin and Legendre (2000), this can be achieved by releasing adult captive-bred individuals, but according to our results, translocating wild individuals arises as an effective alternative that avoids the high economic costs of captive breeding until adulthood. Furthermore, in our case, we released eagles of a wide range of ages, and therefore, higher recruitment rates may be expected if adult releases are prioritized. When not considering budget scenarios (i.e. equal numbers of individuals released by each method, Fig. 1), WildTrans was also the only strategy that prevented long-term extinction. Interestingly, survival estimates for WildTrans birds were slightly lower than for those released by hacking, contrary to what could be expected (Buner & Schaub, 2008; Jule *et al.*, 2008). In this study, WildTrans individuals were sourced after injury and treatment in wildlife rehabilitation centres, which could have decreased the survival prospects of some individuals (Kelly *et al.*, 2010; De La Cruz *et al.*, 2013). Nevertheless, even with decreased survival, the WildTrans strategy showed a better performance than hacking in our simulations, which again may highlight the relevance of greater recruitment to the breeding population and early reproduction for reintroduction success (Morandini *et al.*, 2019).

The effectiveness of different release approaches can greatly vary with different reintroduction scenarios. Detailed case- and species-specific evaluations should be performed to choose an adequate strategy, especially because the strength and duration of post-release effects are known to vary according to species, age, sex, habitat quality and even the timing of releases and individual personality (Moehrenschlager & Macdonald, 2003; Carere & Vanoers, 2004; Tocher *et al.*, 2006; Dickens *et al.*, 2010; Le Gouar *et al.*, 2012; Armstrong *et al.*, 2017). Stress can be a main cause of failure in many reintroductions, and its potentially different effects by age and release methods could further explain the survival differences found in our study (Teixeira *et al.*, 2007; Dickens *et al.*, 2010). When wild-reared non-juveniles are relocated (i.e. WildTrans), they are subject to continuous stressors throughout capture, manipulation, transport, captivity and release into a novel environment. As a result, individuals usually are chronically stressed for weeks, months or even years after release (Dickens *et al.*, 2010; Armstrong *et al.*, 2017). Chronic stress affects cognitive skills and limits the ability of individuals to interact with conspecifics, find environmental cues and learn and remember the location of relevant resources for survival and reproduction, which altogether increase mortality chances (Teixeira *et al.*, 2007). Instead, for captive-reared individuals and birds captured as chicks (i.e. CaptHack, NestHack), the detrimental effects of stress might be milder (Love *et al.*, 2003; Teixeira *et al.*, 2007; Cabezas *et al.*, 2013).

Fast adaptation to novel environments can reduce post-release effects and consequently increase the chances of reintroduction success. This behaviour may be species- or even individual-specific, but it can also depend on the release strategy. Captive rearing (i.e. CaptHack, NestHack) can limit the ability of individuals to fully adapt to wild environments. In particular, for vertebrates that possess a high degree of learned behaviours (i.e. mammals, birds), long-term captivity and the lack of parental care may lead to inability to develop proper predator avoidance or hunting skills, which can lead to increased mortality (Teixeira *et al.*, 2007; Tavecchia *et al.*, 2009). Such effects may be offset with animal training, although this can be a complex option (Griffin *et al.*, 2000). Instead, captive rearing might not have such great impacts in those species with hard-wired behaviour or physiology (Griffiths & Pavajeau, 2008; Cayuela *et al.*, 2019). The age of released individuals can also affect adaptation capacity. In studies involving swift foxes (Moehrenschlager & Macdonald, 2003) and yellow-bellied toads (Cayuela *et al.*, 2019), long-term decreased survival and productivities were detected for released adults in respect to released immatures. Unfortunately, because of our relatively low sample size, we cannot test to which extent these events are affecting our population. Nevertheless, for raptors and many long-lived species survival and productivity are expected to increase with age as a result of experience gains in several skills (i.e. foraging, reproduction, territory acquisition, flight ability, dispersal, etc.) (Sergio *et al.*, 2014). Productivity is usually driven by population density and intraspecific competition, which are expected to be low in reintroduced populations. Hence, negative effects in adult productivity and survival are unlikely to offset the benefits of early reproduction and recruitment provided by non-juvenile releases, as found in this study and Sarrazin and Legendre (2000).

A major concern in raptor translocations when wild-reared individuals are used is post-release dispersal, that is, the permanent movement of released individuals away from the reintroduction area shortly after release. Specifically, most raptor species show strong tenacity to their areas of origin (i.e. ‘homing behaviour’), which may prevent them from establishing in release sites. This issue is usually prevented by using the hacking method, because the feeding and care of fledglings in the reintroduction area during the last stages of growth can promote imprinting to the site and deter dispersal (Amar et al., 2008; Martínez-Abraín *et al.*, 2001). Post-release dispersal was not a major issue in our study reintroduction, as all WildTrans individuals were recontacted after release. In our case, the reintroduction area was an island separated by more than 150 km from the continent (the closest area with an established population). Both natural barriers and long distances between home and release areas are known to promote establishment at reintroduction areas (Van Vuren *et al.*, 1997; Moehrenschlager & Macdonald, 2003). On the other hand, post-release dispersal has also been reported when captive-bred raptors have been released, especially in social species (Mihoub *et al.*, 2014). This behaviour has been described in a wide range of taxa, including mammals (Spinola *et al.*, 2008), birds (Hardman & Moro, 2006), reptiles and amphibians (Germano & Bishop, 2009), fishes (Hervas *et al.*, 2010) and arthropods (Knisley *et al.*, 2005), and might also be affected by the age and sex of released individuals (Moehrenschlager & Macdonald, 2003; Le Gouar *et al.*, 2012). Managers should account for these potential effects in reintroduction planning when age- and sex-specific dispersal patterns in the species to release have been already observed in natural populations (i.e. Nussey *et al.*, 2006; Spinola *et al.*, 2008; Le Gouar *et al.*, 2012).

As quantified here, avoiding the costs of captive breeding can provide important economic savings to reintroduction programmes and economic differences may also increase if we consider further expenses not accounted for in this study. In our specific scenario, we took advantage of wildlife rehabilitation centres to secure wild individuals for WildTrans and active monitoring campaigns to obtain chicks for the NestHack strategy. Even if monitoring and trapping sessions had to be financed to capture such wild individuals, these costs would be very unlikely to exceed the expenses related with the launching and maintenance of breeding programmes (Moran *et al.*, 2005; Ferrer *et al.*, 2018). Therefore, our cost assessments are probably conservative. However, the use of wild-born individuals for both hacking and non-juvenile translocations may present specific challenges that can limit their use. First, healthy source populations for capture or nest-removal may not always be available, especially considering that several target species for reintroduction are endangered throughout their ranges. Detailed evaluation of the impact of extractions to the donor population might be necessary, especially if extractions are intense or continued through time (Ferrer *et al.*, 2014). In contrast, captive breeding programmes may ensure a regular pool of individuals for release and can be of critical importance to ensure the persistence of severely endangered populations. Second, capturing wild individuals or extracting wild chicks from nests may be technically difficult and imply exhaustive monitoring campaigns. In this sense, it is essential to design methods that ensure a large enough number of individuals for release throughout the reintroduction period, as this can be crucial for reintroduction success (Fischer & Lindenmayer, 2000; Rummel *et al.*, 2016). For WildTrans strategies, wildlife recovery centres can be a suitable source of individuals for release, although such a collaboration may require a high level of coordination between centres and reintroduction managers. Third, captive breeding programmes usually have a stronger potential than other alternatives to educate the general public on nature conservation and raise funds (Wiese *et al.*, 1996). Hence, the choice of a reintroduction strategy should be made after careful evaluation of pros and cons of all alternatives.

Conservation managers often face considerable uncertainties when designing and addressing reintroductions, yet important decisions must be made at many stages (Armstrong & Seddon, 2008). For most threatened species, there are considerable knowledge gaps around their population dynamics, ecological requirements and the effects of captivity and stress on their behaviours (Dickens *et al.*, 2010; Nichols & Armstrong, 2012). Luckily, reintroduction programmes are generally not implemented in a single stage but are rather iterated schemes in which the outcomes of initial decisions can be evaluated to improve management in further steps (Varley & Boyce, 2006; Runge, 2013). In this respect, adaptive management and decision theory have proved to be useful tools to making optimal decisions at the initial and other steps of reintroduction while accounting for the uncertainty present at every step (McCarthy & Possingham, 2007). Such approaches often rely on quantitative methods to guide management (Runge, 2011). In our case, modelling and simulations have provided support for WildTrans as the most desirable strategy to achieve success in the reintroduction of the Bonelli's eagle in Mallorca. However, our small sample size limited the degree of detail of our analyses, as usually happens in imperilled populations. In these cases, intensive, long-time population monitoring is essential to extract detailed insights on population dynamics and trends and support evidence-based decisions (Badia-Boher *et al.*, 2019).

In summary, the translocation of wild-reared, non-juvenile individuals (WildTrans) should be considered as a potentially cost-effective strategy in animal reintroductions. Particularly, the use of non-juveniles can promote recruitment to the breeding population and early reproduction, which can be key for reintroduction success. However, post-release effects of different reintroduction strategies can vary depending on species, age, sex and the particularities of the release area, and therefore practitioners should undertake careful evaluation of the pros and cons of all alternatives. As for raptors, when hacking is chosen, we recommend analysing cost-effective alternatives to implementing captive breeding programmes such as the use of chicks extracted from wild nests from healthy populations. As a final consideration, further research is needed to identify cost-effective strategies from an evidence-based perspective. This fact can contribute to a more efficient use of economic and technical resources and an increase in the global effectiveness of conservation schemes, which is essential to deliver an effective response in light of the current biodiversity crisis.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Supplementary file that provides additional information about 1) definition and selection of the multistate analyses ("Multievent Definition and Selection"), 2) the methods used to estimate the economic costs of every release method ("Economic Estimations"), 3) the structure of the individual-based population model ("Population Modelling"), and 4) additional populations simulations that include parametric uncertainty ("Simulations with parametric uncertainty").

Fig S1. Cost calculation representation of all three release methods.

Fig S2. Diagram representing the different steps considered by our individual-based analysis simulating the long-term population dynamics of the reintroduction of the Bonelli's eagle in the island of Mallorca.

Fig S3. Comparison of the effects of hacking and WildTrans reintroductions on long-term population viability with parametric uncertainty on adult survival and adult productivity.

Fig S4. Cost-effectiveness comparison of the effects of WildTrans, NestHack and CaptHack reintroductions on long-term population viability under different budget scenarios and accounting for parametric uncertainty in adult survival and adult productivity.

Supporting Information (Data S1)

Badia-Boher, J.A., Hernández-Matías, A., Viada, C., & Real, J.

Raptor reintroductions: cost-effective alternatives to captive breeding.

Multievent Definition and Selection

Analysis for hacking eagles and wild eagles born in the reintroduction area

We built a global transition matrix considering GPS tag failure (β), recruitment (η) and survival probabilities (S). We defined 7 states: 1) non-territorial live birds with active GPS tags (NTLA), 2) non-territorial live birds with inactive GPS tags (NTLI), 3) territorial live birds with active GPS tags (TLA), 4) territorial live birds with inactive GPS tags (TLI), 5) dead birds with active GPS tags (DA), 6) dead birds with inactive GPS tags (DI) and 7) long-dead birds (LD). The long-dead state is created for modelling purposes, and it indicates that an individual died in a previous occasion and will not be observable in the future.

$$\left(\begin{array}{cccccccc}
 & NTLA & NTLI & TLA & TLI & DA & DI & LD \\
NTLA & S(1-\beta)(1-\eta) & S\beta(1-\eta) & S(1-\beta)\eta & S\beta\eta & (1-S)(1-\beta) & (1-S)\beta & 0 \\
NTLI & 0 & S(1-\eta) & 0 & S\eta & 0 & (1-S) & 0 \\
TLA & 0 & 0 & S(1-\beta) & S\beta & (1-S)(1-\beta) & (1-S)\beta & 0 \\
TLI & 0 & 0 & 0 & S & 0 & (1-S) & 0 \\
DA & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DI & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
LD & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}\right)$$

The general model considered for model selection accounted for an age effect consisting of four age classes (1-year-old, 2-year-old, 3-year-old and >3-year-old) in GPS tag failure, recruitment, and survival probabilities. For GPS tag failure, the term “age effect” refers to the number of years of use of the device, and not to the age of the individuals. Time effects on the estimated parameters could not be considered due to our small sample size. We started our stepwise procedure by testing the GPS failure parameter, in which the best structure included three age classes. Therefore, we used this model as the base for modelling recruitment, in which a three age-class structure was selected. From this model, we compared 6 survival structures linked to the age and territorial status of the eagles (Table 1). The best model considered survival solely dependent on age for the first and second year of life and an interaction between age and recruiting status for older individuals. However, this model estimates survival at 0 for three-year-old and older individuals, which is biologically unrealistic given the high amount of observed surviving birds at that age and is explained by the reduced amount of data available. In contrast, the survival structure and parameter estimations in the second model in the rank matched the available demographic knowledge on the species, and therefore we selected it. The model estimated a low survival probability for one-year-olds (quarterly survival = 0.8543; 95%CI = 0.7723 – 0.9125; annual survival = 0.5238), which increased to a constant probability for two and three-year-olds (0.9314; 95%CI = 0.8311 – 0.9740; annual survival = 0.7527) and higher values from the fourth year onwards. Since all detected individuals aged four and older survived, we cannot provide estimates for these age classes. Recruitment probabilities increased with age from one-year-olds (quarterly recruitment = 0.0731; 95%CI = 0.0332 – 0.1534; annual recruitment = 0.2621) to two-year-olds (quarterly recruitment = 0.1111; 95%CI = 0.0362 – 0.2933; annual recruitment = 0.3757). It was not possible to obtain estimates of recruitment probabilities for older individuals.

Analysis of wild non-juvenile translocated eagles

We considered 4 states: 1) non-territorial live birds (NTL), 2) territorial live birds (TL), 3) dead birds (D), 4) long-dead birds (LD).

$$\begin{pmatrix} & NTL & TL & D & LD \\ NTL & S(1-\eta) & S\eta & (1-S) & 0 \\ TL & 0 & S & (1-S) & 0 \\ D & 0 & 0 & 0 & 1 \\ LD & 0 & 0 & 0 & 1 \end{pmatrix}$$

Starting from a general model with 4 age classes for recruitment (η) and survival (S), we selected the model with the best structure for recruitment probability, which was estimated as constant. From this model, we evaluated four different structures for survival (Table 2). The best model according to the AICc rank showed constant survival from the second year of life onwards. However, this model estimated survival to decrease from the first to the rest of years of age, contrarily to what was observed in the field (all three-year-old and older individuals survived) and to what is expected according to the extensive knowledge on the demographic features of this and other long-lived species. Therefore, we selected the second model in the rank. This model showed a low survival probability for one-year-old individuals (quarterly survival = 0.8286, 95%CI = 0.6674 – 0.9209; annual survival = 0.4714), which increased for two-year-olds (quarterly survival = 0.9229; 95%CI = 0.6090 – 0.9892; annual survival = 0.7256) and was higher and constant for older individuals. Due to the low sample size available, we cannot provide survival estimates for these individuals. Recruitment probabilities in this model were estimated as constant (quarterly recruitment = 0.1669; 95%CI = 0.0712 – 0.3436; annual recruitment = 0.5184).

Economic Estimations

We estimated the individual costs of eagles released by every of the three evaluated methods. We accounted for the personnel and bird feeding costs funded by the reintroduction programme until the last day of post-release supplementary feeding. Infrastructure and maintenance costs, as well as other expenses external to the programme, were not accounted for. Criteria for economic quantification and estimations for all three release methods are described hereunder and are summarized in Figure S1.

i. <u>The hacking method: captive-breeding (CaptHack) and nest-extracted (NestHack) individuals.</u>

We estimated the costs of releasing eagles by every of the two hacking methods based on the costs reported at the reintroduction area. Captive-breeding birds were born and raised in a range of different breeding centres following the hacking method before being transferred to the release area in Mallorca, where hacking continued until release. Similarly, nest-extracted birds were first sent to different breeding centres before handoff to Mallorca. Thus, obtaining precise cost estimates from every centre was not possible, and therefore we assumed the daily costs related to the implementation of hacking at the reintroduction area in Mallorca for the whole hacking period of every individual.

We accounted for personnel and feeding costs. To do so, we first calculated hacking costs in the release area in Mallorca. For personnel, implementing hacking and post-release supplementary feeding in the release area involved a total cost of 150 €/day. Hacking campaigns in Mallorca lasted for 105 days per year on average, and the average number of hacked birds per campaign was 4.5. This provided a dedication of 23.3 days / eagle on the island. For feeding costs, animals were fed with pigeons (0.8 pieces per eagle per day) at a cost of 2.5€ / pigeon. This amounts a daily cost of 2 € / eagle

For hacking birds original from breeding centres (CaptHack), we accounted for costs starting from the birth of the eagle. Individuals spent 50 days on average before being transferred to Mallorca. Therefore, by summing these 50 days to the 23.3 days on average spent in Mallorca, care of captive-breeding hacking individuals extended to 73.3 days. By calculating the daily personnel and feeding costs along this period, the costs per eagle add up to 11142 €.

For nest-extracted birds (NestHack), we did not account for costs related to nest search and monitoring, since we took advantage of an ongoing monitoring programme. We accounted for costs starting from the day eagles were extracted from their nests. Birds were removed from wild nests at the average age of 40 days and immediately transferred to breeding centres to be raised via hacking. Then, they were transferred to Mallorca at the average age of 50 days. Therefore, care for this birds extended to 23.3+10=33.3 days. By calculating personnel and feeding costs along this period, costs per eagle amounted 5062 €.

ii. The translocation of wild-reared non-juvenile individuals (WildTrans)

Individuals were original from wildlife recovery centres, where they had undergone treatment for a range of injuries. Since these centres were external to the programme and recovery costs were covered by the centres, we did not account for such costs. Recovered individuals were sent to the release area, where they spent 5.9 days on average in aviaries before release. Once released, supplementary food was provided for 17.2 days on average. Therefore, care for these birds extended towards 23.1 days on average. Since these individuals were fed the same amount and type of food than hacking individuals, feeding costs were considered identical. Instead, due to the lower care requirements of this method, daily personnel costs were lower (100 € / day). Therefore, personnel costs were estimated at 2310 € / eagle and feeding costs at 28.875 € / eagle, which amounted to 2339 € / eagle.

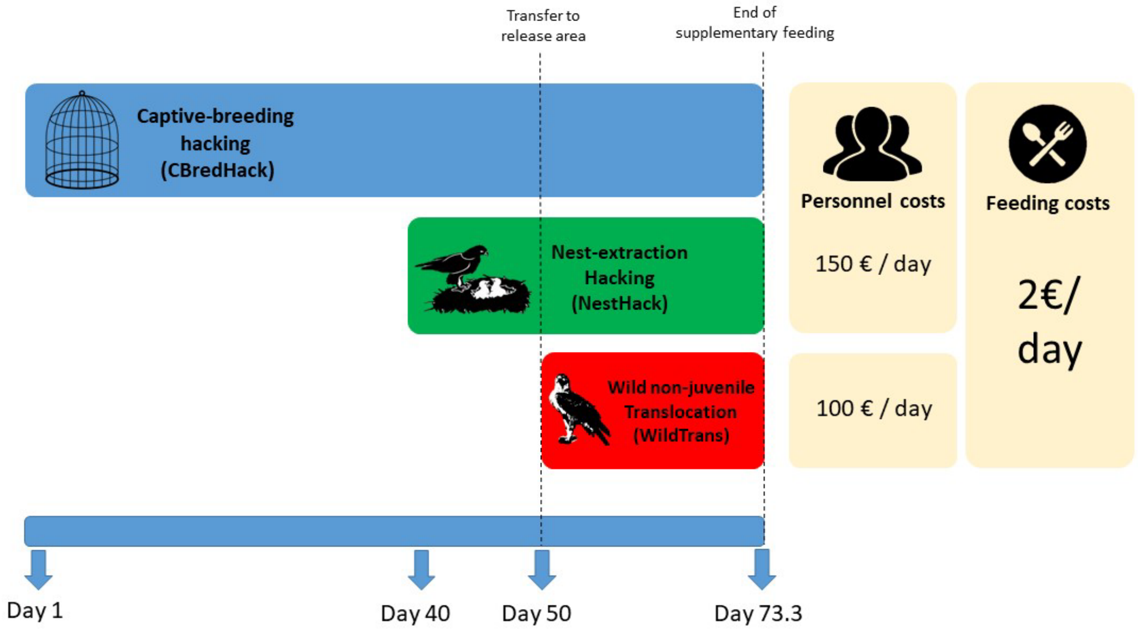

Figure S1. Cost calculation representation of all three release methods. Lower blue bar indicates the average duration in days of eagle care for every method. The avg. eagle care durations of NestHack (33.3 avg. days) and WNJTrans (23.3 avg. days) are displayed in reference to the duration of CaptHack (73.3 avg. days). Daily costs are calculated and extended towards the avg. days of care of eagles by every method. Personnel costs were equal for CaptHack and NestHack methods (i.e., 150 €/day) and lower for the WildTrans strategy (100 €/day). Feeding costs were equal for all eagles of all methods (2 €/day).

Population Modelling

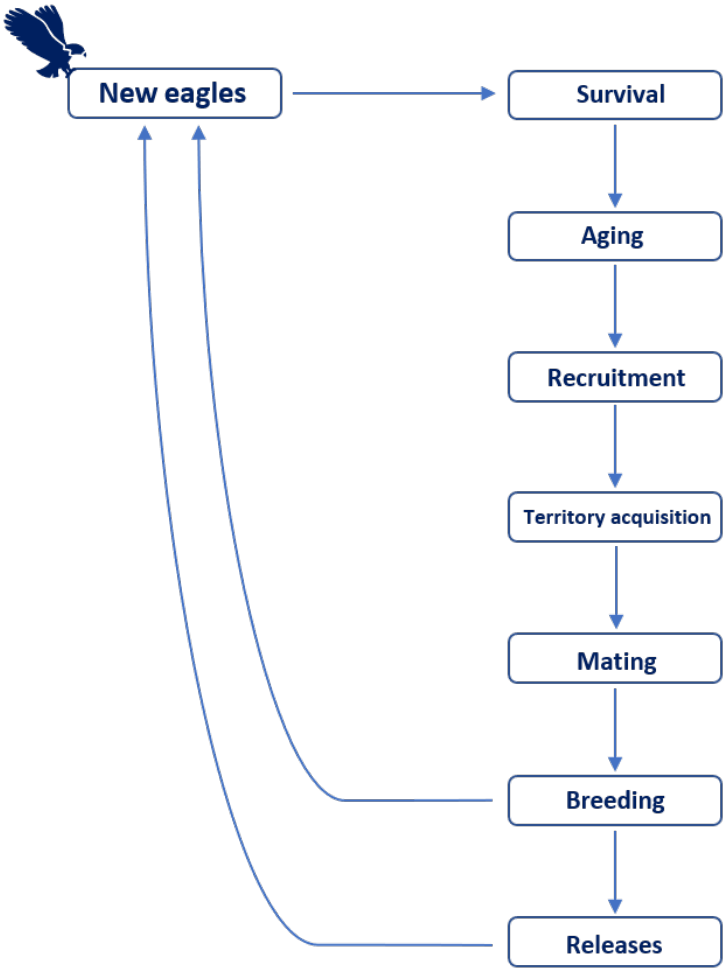

Figure S2. Diagram representing the different steps considered by our individual-based analysis simulating the long-term population dynamics of the reintroduction of the Bonelli's eagle in the island of Mallorca.

Simulations with parametric uncertainty

Reintroduced or highly threatened populations usually require urgent population analyses to draw predictions about their fate and recommendations about their management. However, due to the low sample sizes of these populations, quantitative data are usually scarce, and the statistical power of population analyses is limited. Using maximum-likelihood estimators in population models can lead to optimistic outcomes and overconfidence in drawing conclusions from results (Morris and Doak, 2002). To assess how parametric uncertainty could be affecting our population models we ran our simulations with parametric uncertainty in main vital rates (i.e., those of adults - adult survival and adult productivity). To do so, we drew sampling variance estimates from conspecific continental populations (Hernández-Matías et al., 2013). Adult survival and adult productivity variances were estimated as averages of variances of continental populations (0.00024 and 0.03269 respectively). We accounted for the variances in our code following Morris and Doak (2002) and McGowan et al. (2011): we generated random survival and productivity values for each iteration in the simulation following a beta distribution based on the mean and sampling variance of each parameter. We implemented these variations in both our models with and without costs following the same settings as the rest of models, with 1000 iterations, 50-year runs and releases for the first 10 years.

Results – Hacking vs. WildTrans effect on reintroduction success

WildTrans showed higher mean numbers of pairs for the whole 50-year simulation (Figure S3), with biggest differences in early stages (year 20: WildTrans 14.53 pairs 95%CI 4-25 vs. Hacking 11.22 pairs 95%CI 2-25; year 50: WildTrans 18.79 pairs 95%CI 0-25 vs. Hacking 17.36 pairs 95%CI 0-25). As expected when parametric uncertainty is accounted for (Morris and Doak, 2002), our results show bigger uncertainties and wider confidence intervals, to the extent that no method can guarantee population persistence in the long term. Still, while in the hacking scenario confidence intervals reach 0 at simulation year 29, in WildTrans this happens 8 years later. Therefore, although the addition of parametric uncertainty evidences the need to obtain high precision in parameter estimations, WildTrans still shows an important trend for a higher effectiveness, which maximizes in the early stages of the reintroduction.

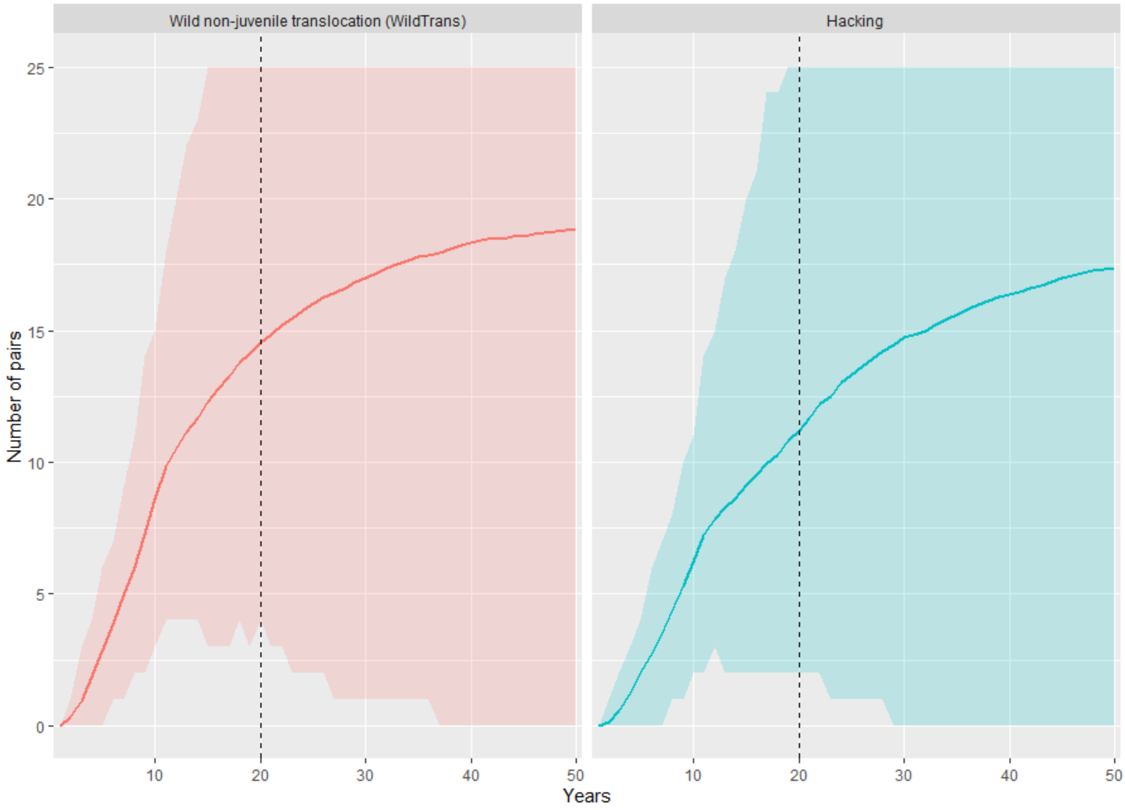

Figure S3. Comparison of the effects of hacking and WildTrans reintroductions on long-term population viability with parametric uncertainty on adult survival and adult productivity. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year and shaded areas indicate 95% confidence intervals.

<u>Results – Cost-effectiveness of CaptHack, NestHack and WildTrans</u>

Again, WildTrans still show highest number of pair averages in all scenarios (Figure S4). When compared to the scenarios where parametric uncertainty is not considered, WildTrans no longer guarantees long-term persistence within the lowest budget scenario (i.e., 15000 €/year) (Year 50: WildTrans 20.1 pairs IC95% 0-25, NestHack 12.6 pairs IC95% 0-25, CaptHack 7.6 pairs IC95% 0-25). However, WildTrans still prevents long-term extinction in the mid-budget scenario (Year 50: WildTrans 22.9 pairs IC95% 4-25, NestHack 18.2 pairs IC95% 0-25, CaptHack 16.2 pairs IC95% 0-25) and high-budget scenario (Year 50: WildTrans 24.0 IC95% 10-25, NestHack 21.6 IC95% 0-25, CaptHack 16.1 IC95% 0-25). Instead, while NestHack prevented long-term extinction with certainty within the highest budget when no parametric uncertainty was considered, now long-term extinction cannot be discarded within any of the proposed budgets. Again, CaptHack shows the lowest average numbers of pairs of all strategies.

Although the addition of parametric uncertainty has changed some results within scenarios, there are no significant cost-effectivenes changes between strategies. Again, results suggest WildTrans is the most cost-effective strategy followed by NestHack and lastly by CaptHack. Therefore, we believe that the main conclusion about the effectiveness of wild-reared non-juvenile releases in animal translocations is sustained by our analyses.

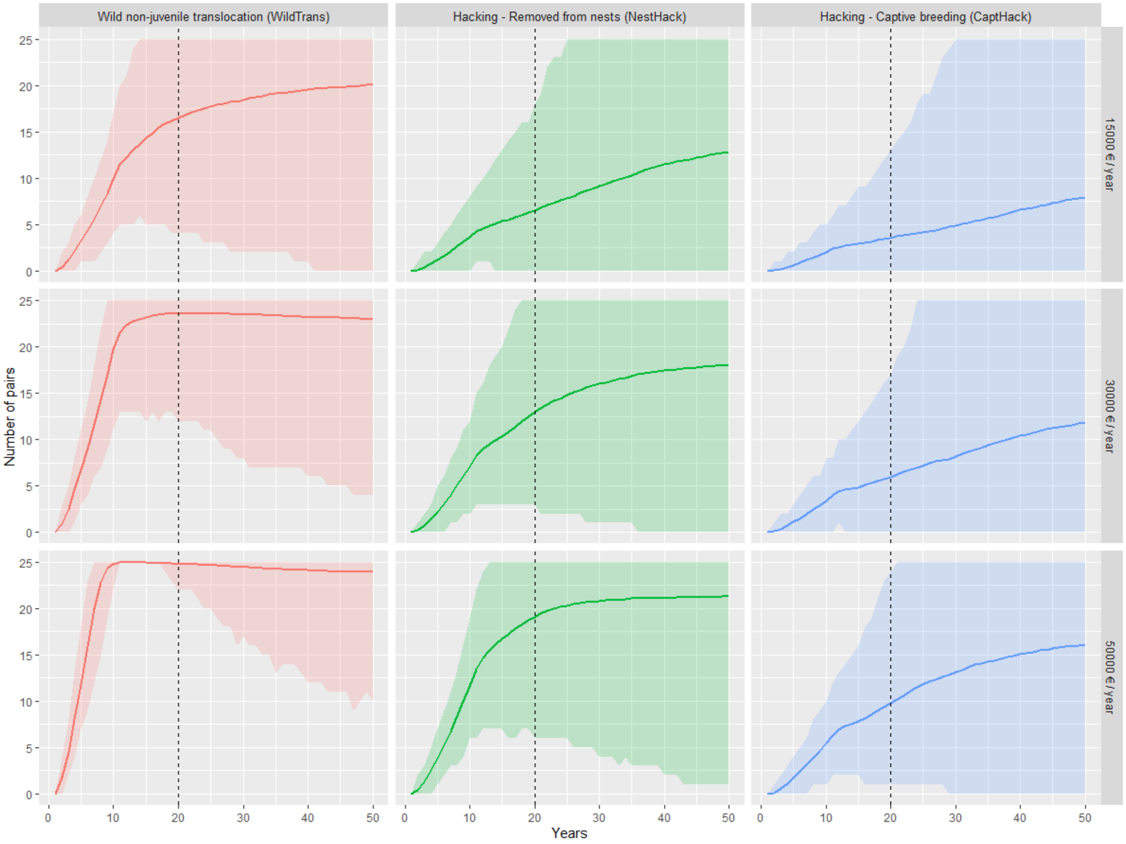

Figure S4. Cost-effectiveness comparison of the effects of WildTrans, NestHack and CaptHack reintroductions on long-term population viability under different budget scenarios and accounting for parametric uncertainty in adult survival and adult productivity. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year and shaded areas indicate 95% confidence intervals.

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CHAPTER 2

Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses

Photograph courtesy of Jaume Elies

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Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses

Jaume A. Badia-Boher[1]✉, Joan Real[1], Joan Lluís Riera[1], Frederic Bartumeus[2,3,4], Francesc Parés[1], Josep Maria Bas[5] & Antonio Hernández-Matías[1]

Robust and reliable estimates of demographic parameters are essential to understand population dynamics. Natal dispersal is a common process in monitored populations and can cause underestimations of survival and dispersal due to permanent emigration. Here, we present a multistate Bayesian capture-mark-recapture approach based on a joint estimation of natal dispersal kernel and detection probabilities to address biases in survival, dispersal, and related demographic parameters when dispersal information is limited. We implement this approach to long-term data of a threatened population: the Bonelli's eagle in Catalonia (SW Europe). To assess the method's performance, we compare demographic estimates structured by sex, age, and breeding status in cases of limited versus large data scales, with those of classical models where dispersal and detection probabilities are estimated separately. Results show substantial corrections of demographic estimates. Natal dispersal and permanent emigration probabilities were larger in females, and consequently, female non-breeder survival showed larger differences between separate and joint estimation models. Moreover, our results suggest that estimates are sensitive to the choice of the dispersal kernel, fat-tailed kernels providing larger values in cases of data limitation. This study provides a general multistate framework to model demographic parameters while correcting permanent emigration biases caused by natal dispersal.

Understanding the drivers of population dynamics is key in basic and applied ecology. Survival is a vital rate that describes the probability of an individual to survive for a given time period and is a major contributor to population growth rate[1]. Dispersal is the movement of individuals from their birth site to their breeding site (natal dispersal) as well as among breeding sites (breeding dispersal)[2] and has deep implications in population dynamics, from determining emigration to regulating gene flow, inbreeding avoidance, responses to environmental pressures, metapopulation persistence, and source-sink dynamics[3–6]. Consequently, both survival and dispersal processes are central demographic features that carry serious eco-evolutionary implications[1,4]. Thus, obtaining robust and unbiased estimates of both parameters in ecological studies is essential to increase our knowledge about population processes. In addition, this knowledge is crucial to correctly assess the conservation status of populations and design effective case-specific management actions[7,8], which is essential to guide conservation measures in the urge to alleviate the global biodiversity crisis[9].

The capture-mark-recapture (CMR) method is widely used in survival estimation[10]. This approach is based on the statistical analysis of monitoring data of marked populations and permits a separate estimation of survival and detection probabilities, which is an essential first step to provide unbiased estimates of survival. In the last decades, analytical advances addressed some limitations and violations of the traditional assumptions of CMR models, such as tag loss[11], detection and survival heterogeneity[12], and instantaneous sampling periods[13]. In addition, multistate models allowed for greater flexibility in modelling complex systems, while multievent

[1]Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia I Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain. [2]Centre for Advanced Studies of Blanes (CEAB-CSIC), Blanes, Spain. [3]Centre for Research on Ecology and Forestry Applications (CREAF), Cerdanyola del Vallès, Barcelona, Spain. [4]Catalan Institute for Research and Advanced Studies (ICREA), Barcelona, Spain. [5]Animal Biology Lab & BioLand, Departament de Ciències Ambientals, Universitat de Girona, Girona, Spain. ✉email: jabadia@ub.edu

models enabled dealing with uncertainty in states' assignments[14]. However, a still problematic limitation of CMR analyses that may lead to considerable biases in demographic parameters is the presence of emigration from the study area, which is a very common process in animal populations[15,16]. If emigration is temporary and random, only detection probabilities become biased[17]. Instead, if emigration is permanent (that is, individuals that leave the study area do not return), models cannot distinguish between emigration and mortality, which leads to an underestimation of survival[18]. Traditionally, this has been accounted for by reporting apparent survival, which is the product of true survival and study area fidelity[10]. In populations where permanent emigration is present, site fidelity is always lower than 1, which makes apparent survival be lower than true survival. In addition, apparent survival has no clear biological meaning, and if estimated with time, sex or age variation, differences in apparent survival among population fractions might correspond to variations in dispersal behaviour and not to true survival differences[18,19]. In the last decades, solutions that estimate survival and site fidelity without explicitly modelling dispersal have been presented[20–22]. However, such designs rely on the availability of additional data, such as observations outside the study area or within sampling occasions, or tag recoveries.

Other alternatives to overcome this bias have focused on explicitly modelling dispersal processes in survival analyses[23]. However, the main challenge in modelling dispersal data obtained from the monitoring of ringed populations is that the resulting dispersal distances generally lead to underestimations of the dispersal kernels of study populations, as some dispersal events (typically the ones ending outside the study area) are rarely detected. Indeed, observed dispersal kernels are a result of the interplay between the true dispersal kernel and detection probabilities, which may be heterogeneous and highly variable across the dispersal range of the species[24,25]. This is due to (1) the border effect, which makes individuals born closer to the limit of the study area more likely to emigrate permanently and therefore remain undetected in subsequent sampling periods[24,26]; and (2) because study areas are finite and limited in respect to the species dispersal capacity, which makes long-distance dispersal events impossible or unlikely to be observed and accounted for in dispersal kernels[8].

The development of Bayesian hierarchical CMR models (e.g.,[27]) has provided a novel, powerful framework to address these biases[28]. A good example is the Bayesian spatial extension of the Cormack–Jolly–Seber CMR model developed by[26]. This method links the dispersal and observation processes to obtain true survival estimates accounting for emigration probabilities along with corrected dispersal kernels. Nevertheless, spatial CMR models rarely differentiate between natal and breeding dispersal (but see[6]). This apparently subtle difference can have important implications for the robustness of the estimated demographic parameters, as in most species breeding and natal dispersal have different implications for population dynamics[2,8,29]. Generally, natal dispersal distances are larger and involve most or all long-distance movements in a population, which are more likely to fall outside the boundaries of study areas and remain unobserved[5,8,29]. Therefore, natal dispersal is most often the main driver of permanent emigration and may have dramatic effects on the overall dynamics of local populations and metapopulations over broad areas[3]. As a result, kernels of breeding and natal dispersal usually differ in shape, with natal dispersal ones being heavy-tailed and right-skewed[30]. Therefore, if natal dispersal is not explicitly modelled with adequate long-tailed distributions, dispersal kernels may fail to predict unobserved long-distance natal dispersal movements, which may significantly underestimate the dispersal capacity of the species, and consequently, emigration and survival probabilities[8,29,30]. On the other hand, natal dispersal in birds is usually sex-biased, with females usually dispersing farther away than males[31]. In addition, because natal dispersal is intrinsically linked to sexual maturation, dispersal and related processes can show an age trend in long-lived species. Therefore, such processes should be modelled using age and sex structures to avoid biases in demographic estimates.

The aim of this study is to provide a method to minimize the biases in survival and natal dispersal estimations caused by permanent emigration in CMR analyses. For a widely applicable solution to the issue of permanent emigration, it is essential to design a modelling framework that deals with the most common factors that generate this source of bias: (1) natal dispersal, and (2) the restricted sizes of most study areas, which make such movements unlikely or impossible to be detected, and consequently, generate the biases in dispersal and survival estimates. To do so, we perform a joint estimation of natal dispersal and detection probabilities to infer the true natal dispersal kernel, permanent emigration probabilities, and survival estimates in a Bayesian spatial multistate CMR framework[16,24,26,32]. In addition, we model dispersal under two different statistical distributions, i.e., gamma (short-to-fat tailed depending on parameters) and lognormal (heavier and longer tail than gamma), to stress the importance of distribution choice in generating unbiased parameter estimates[8]. To implement this approach, we used as a case study a population of a long-lived territorial bird, the Bonelli's eagle, located in Catalonia, NE Iberian Peninsula. This study population provides an exceptional scenario to apply the joint estimation approach because: (1) the species shows a very large natal dispersal capacity that can easily exceed the limits of most study areas[33,34]; (2) we carried out an intensive ringing programme over 13 years (ca. 70% of all fledged chicks were tagged in a population holding ca. 6% of the European population); and (3) we benefited from the intensive monitoring of all neighbouring populations of this species, meaning that we could extend our capacity to detect tagged individuals over a broad region covering almost the entire range of this species in Western Europe. In this context, we fitted three different models to assess the performance of our correction method under gamma and lognormal natal dispersal distributions. First, we modelled a scenario in which we included only observations from the study population and performed a classical estimation where detection, survival, and natal dispersal probabilities were not linked for a joint estimation (i.e., "separate estimation"—the SEP-CAT models). Second, we considered only observations from the study population but performed a joint estimation of these parameters (the JOINT-CAT models). Third, we implemented a joint estimation in which all observations of breeding individuals inside and outside the study population were considered (the JOINT-ALL models). This third scenario is expected to provide us the closest approximation to true estimates of survival and natal dispersal kernels, since it is informed by more data on encounters and natal dispersal events over a larger range. Therefore, to assess the effectiveness of the joint estimation method when encounter and natal dispersal data are restricted to the study population, we compared the estimates of JOINT-CAT against those of JOINT-ALL. All models included age and sex structures in survival, recruitment, natal dispersal, and other parameters. Finally, based on the kernels estimated by the models, we performed simulations of natal dispersal movements for each territory and sex to estimate and map continuous probabilities of permanent emigration. The aim of these simulations was to allow a finer-scale evaluation of the sex-specific probabilities of individuals born in each territory to either leave or remain in the study area after natal dispersal.

Results

Global JMV goodness-of-fit tests indicated an adequate fit to the data for both models with observations from the study area only (CAT; $x^2 = 26.613$, df = 26, $p = 0.430$) and models with observations everywhere (ALL; $x^2 = 29.791$, df = 28, $p = 0.373$). All 6 models (i.e., SEP-CAT-Lognormal, SEP-CAT-Gamma, JOINT-CAT-Lognormal, JOINT-CAT-Gamma, JOINT-ALL-Lognormal, and JOINT-ALL-Gamma) reached adequate convergence based on the Gelman-Rubin statistic (Rhat ≤ 1.10 for all parameters) and visual inspection of chain mixing[35].

Natal dispersal estimation showed consistent differences among sexes, with larger distances for females than for males in all scenarios (Tables S1, S2, S3; Figs. 1, 2). Dispersal distances and kernel shapes in JOINT-CAT models approached the estimates provided by JOINT-ALL models and were substantially larger—and considerably more uncertain—than those of SEP-CAT, especially when using lognormal distributions (Fig. 1, Table S2). Female average dispersal distance increased by 16.6 km (89%Highest Posterior Density Interval, HPDI, of the difference = −34.3–74.2) from SEP-CAT to JOINT-CAT models when using gamma distributions, and by 68.7 km (−60.2–237.8) in lognormal models. The average dispersal distance of females estimated by JOINT-CAT with lognormal distributions was higher than that of JOINT-ALL when using gamma distributions (30.4 km difference, −79.8–190.2). In the case of males, distances estimated by JOINT-CAT models increased by 1.6 km (−10.1–13.3) and 8.9 km (−19.9–39.5) in gamma and lognormal distributions respectively, compared to SEP-CAT models.

Estimates of permanent emigration probabilities in the population notably increased from SEP-CAT to JOINT-CAT models but fell short of the values estimated by JOINT-ALL models. Lognormal distributions provided closer values between JOINT-CAT and JOINT-ALL estimates (Fig. 3). Using gamma distributions, estimates increased from 0.23 (89% HPDI = 0.18–0.30) in SEP-CAT to 0.28 (0.21–0.35) in JOINT-CAT and 0.40 (0.34–0.45) in JOINT-ALL, while when using lognormal distributions values grew from 0.26 (0.20–0.33) to 0.35 (0.27–0.43) and 0.39 (0.33–0.44) respectively. Mapped permanent emigration probabilities between sexes showed differences by sex and higher chances of leaving the study area closer to its boundaries (Fig. 4). Males born in central areas showed permanent emigration probabilities below 7%, which increased up to 28% in females. In areas closer to boundaries, probabilities peaked to 40% in males and 60% in females.

Survival estimates of non-breeders showed a clear increase when using joint estimation models, especially in females (Table S1, Fig. 5). Namely, when comparing SEP-CAT and JOINT-CAT lognormal models, female non-breeder survival increased by 0.04 in 1-year-olds (89%HPDI of the difference = −0.1–0.17), 0.06 in 2 and 3-year-olds (−0.08–0.2) and 0.04 (−0.2–0.28) in adults. In males, differences were smaller, with increases of 0.02 (−0.11–0.15) in 1-year-olds, 0.02 (−0.12–0.17) in 2 and 3-year-olds, and 0.01 (−0.15–0.17) in adults. Differences in non-breeder survival between models using gamma and lognormal distributions were especially visible in females. JOINT-CAT lognormal models provided moderately higher values, and closer to those of JOINT-ALL models. On the other hand, survival of breeding birds showed no differences among models and was estimated at 0.87 (0.8–0.94) in females and 0.88 (0.83–0.94) in males (Table S1). Recruitment into the breeding population also showed remarkable differences between separate and joint estimation models in females (Figure S5), while

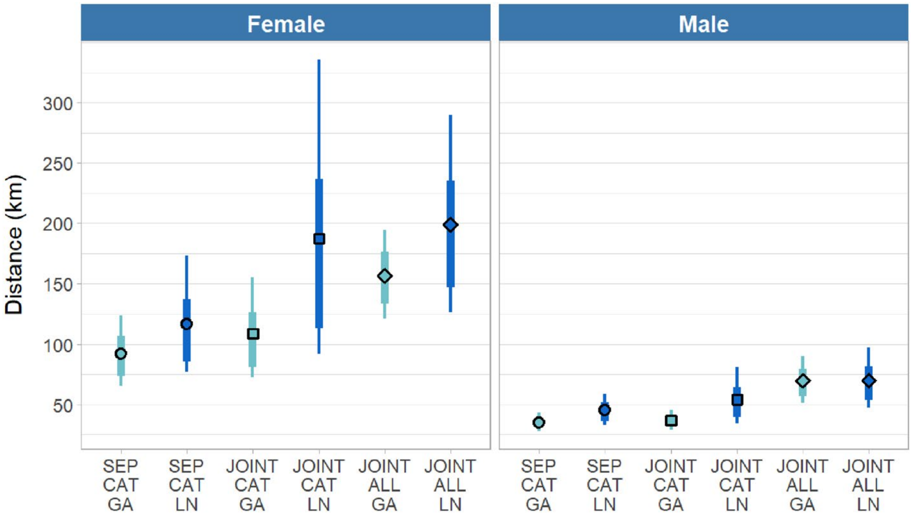

Figure 1. Average natal dispersal distance (km) by model, sex, and distribution (gamma: GA, lognormal: LN). Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

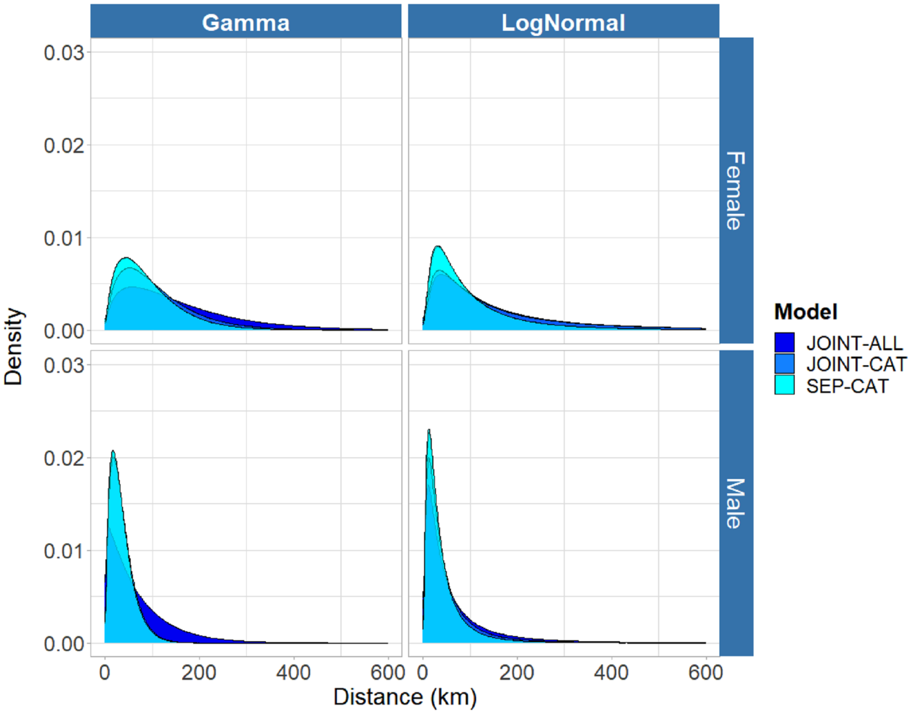

Figure 2. Median natal dispersal kernels (Y: probability density, X: km) by model type, sex, and dispersal distribution.

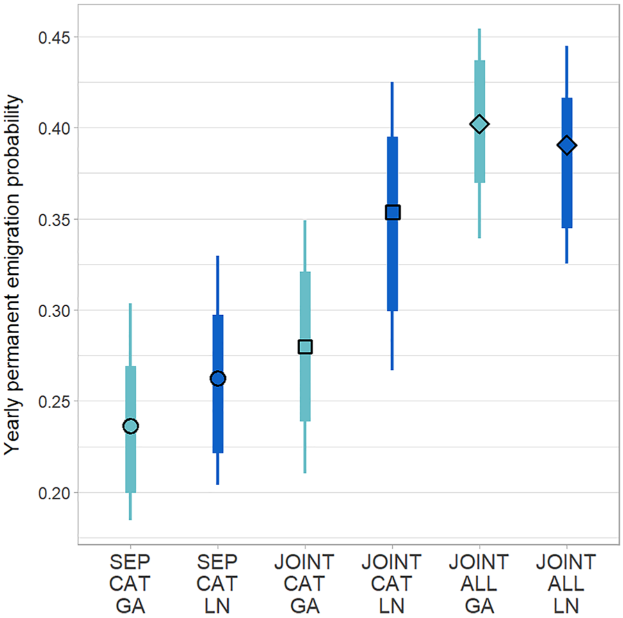

Figure 3. Permanent emigration probability by model and dispersal distribution (gamma: GA, lognormal: LN). Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

male differences were smaller. In all scenarios, females showed the highest recruitment probabilities for 3-year-olds (JOINT-ALL lognormal model, 0.54; 89%HPDI = 0.39–0.70) and adults (0.41; 0.24–0.58). Male recruitment probabilities peaked in 3-year-olds (JOINT-ALL lognormal, 0.46; 0.31–0.61), but considerably decreased in adults (0.13; 0.06–0.37).

Recapture probabilities were estimated at 0.85 (0.65–0.98) for breeders (P_B) and 0.045 (0.035–0.056) for non-breeders (P_{NB}) in all models. Recovery probabilities of dead non-breeders were estimated very similarly across

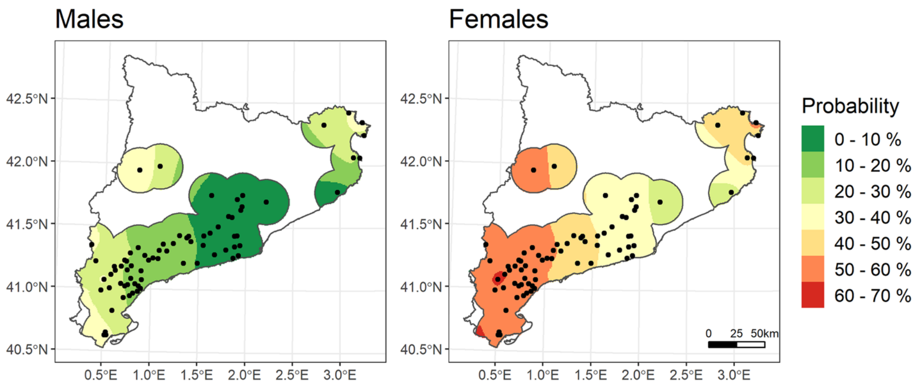

Figure 4. Mean Bonelli's eagle permanent emigration probabilities mapped by sex following a spatial kriging interpolation across the distribution of the study population. Map source: Natural Earth.

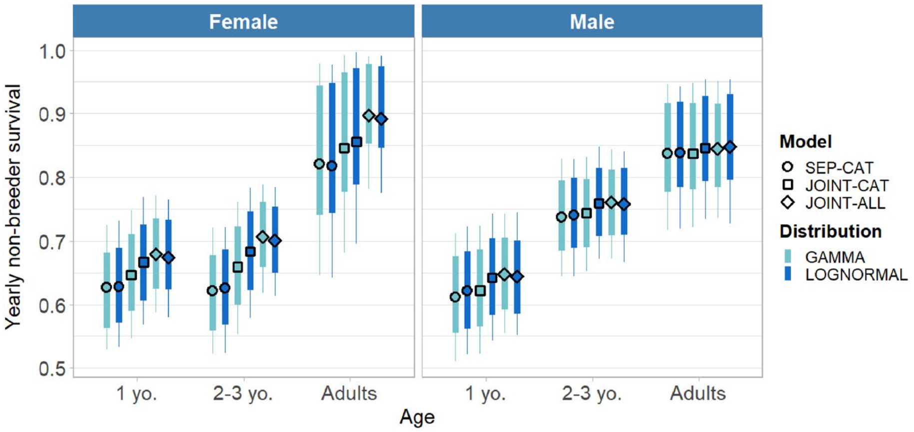

Figure 5. Non-breeder survival by model, age, sex, and distribution. Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

models as well, with around 0.21 (0.18–0.26). Similarly, in breeders, models estimated recovery at around 0.22 (0.12–0.33). Estimates of the effectiveness of different surveying methods at detecting and identifying individuals in territories, which were calculated to deal with breeder detection heterogeneity and incorporated into first-time recapture probabilities of breeders P_{B1} (see *Methods* and subsection *Recapture parameters* for further details), provided a 0.39 (0.37–0.42) probability of detecting a ring when using conventional territory monitoring, 0.84 (0.81–0.88) when using camera-trapping alone, and 0.989 when using both methods altogether (0.985–0.994).

Discussion

Survival and dispersal processes are central demographic features of populations[1,4], though their estimation can be seriously biased by permanent emigration when the dispersal capacities of individuals exceed the dimensions of monitoring areas, a common issue in ecological studies. Here, we present a spatial capture-mark-recapture (CMR) joint estimation approach to model permanent emigration generated by natal dispersal and address subsequent biases in the estimation of dispersal, survival, and other demographic parameters of wild populations. The crucial aspect of this approach is estimating the probabilities of leaving the study area for each marked individual, conditional on their location of birth and natal dispersal distance, and accounting for all modelled sources of uncertainty about the states of the individuals. We applied this method to estimate demographic parameters in a population of a territorial long-lived bird, the Bonelli's eagle, in which permanent emigration was represented as breeding recruitment outside the study area. We utilized an intensive monitoring campaign that covered the entire range of this species in western Europe to compare the estimates of survival and dispersal kernel under three scenarios: (1) models that formulate a classical separate estimation of data restricted to the focal study area (SEP-CAT models), the most common scenario in monitoring schemes; (2) joint estimation of CMR data and dispersal parameters from the focal study area (JOINT-CAT models); and (3) joint estimation of data from the whole W European distribution (JOINT-ALL models), which is expected to provide us the closest approximation to the true parameter estimates. Our results illustrate that the joint estimation approach provides substantial corrections of survival and dispersal estimates even when only data of the focal study area are considered compared to those of the classical separate estimation approach (Figs. 1, 2, 3, 5).

Our confidence in the effectiveness of the joint estimation approach is based on the fundamental assumption that JOINT-ALL models provide the closest approximation to the true estimates. Indeed, JOINT-ALL models include dispersal and recapture data from the whole range of the Bonelli's eagle in W Europe. This fact diminishes the effects of censoring on dispersal data: as the study area expands, the chance of observing more dispersal movements and at longer distances increases. In the case of our study, maximum observed natal dispersal distances in the focal study area were 95 km for males and 271 km for females but increased to 500 and 490 km respectively when all data were considered. Hence, the ability of the models that link survival and observation processes to approximate true survival, natal dispersal kernels, and permanent emigration probabilities is enhanced[24,26,32]. Thus, we consider that using JOINT-ALL as a reference model from which to assess the effectiveness of joint estimation methods in cases of limited and truncated data (i.e., JOINT-CAT models) is a robust strategy.

Animal populations are composed of individuals that may show differences in survival and dispersal according to their age, sex, and breeding status. Such intrapopulation heterogeneity may carry important consequences for population dynamics[36]. Our results highlight that the permanent emigration biases may be more intense in specific age classes (Table S1, Fig. 5). In addition, we found that survival estimates of non-breeders are sensitive to the permanent emigration bias. This fact should be expected for many animal species, as non-breeders often undertake the longest movements in their lives (natal dispersal) right before first breeding. Non-breeding fractions of populations have a key role in population regulation and stability, and therefore biased survival estimates may lead to inaccurate assessments of the status and prospects of whole animal populations[37]. Specifically, Hernández-Matías et al.[38] showed that a survival increase of ca. 8% in non-breeders would turn our study population from decreasing to self-sustaining. According to our results, survival differences of such magnitude can be generated by permanent emigration biases, especially in females. Indeed, female survival was systematically higher in JOINT-CAT compared to SEP-CAT models, differing by 0.04 in 1-year-olds, 0.06 in 2 and 3-year-olds and 0.04 in adults when using lognormal models, and differences with JOINT-ALL models are around 0.08 in 2 and 3-year-olds and adults. In this line, our results showed more intense survival biases in females than in males, which is related to the fact that females show larger natal dispersal and thus higher propensity to permanent emigration. Sex differences in natal dispersal are common in wild populations[39]. Thus, if demographic parameters are estimated without considering permanent emigration and sex-structured dispersal, the resulting sex differences in apparent survival estimates may actually be signalling differences in dispersal behaviour and site fidelity rather than true survival differences[19]. Furthermore, our results show that permanent emigration biases can also affect estimates of the age of sexual maturity (i.e., recruitment in this study). Unbiased estimates of sexual maturity are essential in models of population viability, as population growth rates may be very sensitive to them[40]. In summary, our findings suggest that the potential of permanent emigration to cause bias in ecological studies, as well as population and species assessments, should not be neglected. Hence, study designs accounting for permanent emigration should be implemented in demographic studies whenever possible, especially in species with long dispersal capacities. It is true that bias correction in demographic parameters may not be complete in cases of limited data as in the JOINT-CAT scenario (Table S1). However, substantial bias reductions as the ones found here may help improving the accuracy of subsequent analyses based on these estimates, such as population viability analyses, integrated population models or assessments of conservation status.

Dispersal has deep implications in eco-evolutionary processes[5,6]. However, long-distance dispersal movements are difficult to detect in many study systems, and therefore, obtaining unbiased estimates of dispersal kernels may be challenging. Interestingly, our findings emphasize that the method presented here is sensitive to the choice of the dispersal distribution. In the case of JOINT-ALL models, results are almost identical when using gamma and lognormal distributions. This suggests that whenever larger amounts of data are available from a wider geographical range, both distributions provide very similar corrections of demographic parameters, even if the shapes of the dispersal kernels differ (Tables S1, S2, S3; Figs. 2, 3). However, our results show that when the dispersal data are strongly truncated as a result of only having data from the focal study area available (i.e., the most common scenario in ecological studies, represented by SEP-CAT and JOINT-CAT), joint-estimation models (JOINT-CAT) provide closer estimates of all demographic estimates to JOINT-ALL when lognormal distributions are used. This effect is particularly visible in average natal dispersal and permanent emigration estimates, which are considerably higher in JOINT-CAT lognormal than in JOINT-CAT gamma, and notably closer to JOINT-ALL estimates. A reasonable explanation is that lognormal distributions are heavy-tailed and thus may provide larger probabilities for long-distance dispersal movements even when these have been poorly detected[8,25,29]. This rationale would match the recent findings of Fandos et al.[41], who found that long-distance dispersal movements were frequent across bird species, and dispersal kernels were generally better represented by heavy-tailed distributions. This suggests that heavy-tailed distributions can generally be more adequate when modelling natal dispersal in joint estimation formulations. However, given that in many study cases there may be little to no information about the shape and the tail-end of the true natal dispersal kernel, providing model results under different dispersal distributions may be a more conservative choice[3,8,29,41]. In ideal cases where unbiased dispersal data are available (i.e., telemetry or different dispersal estimation methods), these should be primarily considered for the choice of adequate natal dispersal distributions.

For a widely applicable solution to the issue of permanent emigration, it is essential that our modelling framework is easily extrapolated to other study systems. In basic terms, our modelling approach consists of a multistate CMR submodel and a spatial submodel appropriately linked to infer permanent emigration probabilities. Here, we incorporated some modelling specificities to account for the particularities of our study system such as territorial behaviour, delayed maturity, detection heterogeneity in breeders, or the possibility to encounter dead individuals. However, all these characteristics can be easily modified to handle a wide range of multistate formulations either simpler or more complex, taking advantage of the wide flexibility of Bayesian hierarchical models (see Appendix S3 and Figures S6 to S11 therein, where we present a brief guide to adapt the joint estimation formulation to other study designs, starting by the simplest possible designs and moving to examples without detection heterogeneity and dead recoveries). The Joint Estimation approach may be useful for species where individuals are tagged at the natal site, and for which a fraction of all dispersing individuals may disperse outside the study area. A key point is to be able to model a species or population distribution range to the extent it encompasses the dispersal capacity of the population. In cases where the range is not known, multiple methods are available to estimate it[42]. In our example, territory locations were known with certainty or simulated following distribution and census data. In territorial species where territory locations cannot be estimated, or in species whose space use is not structured into territories, space may be divided into grids with detection probabilities assigned depending on their location (i.e., inside or outside a study area;[26]). Isotropical dispersal kernels are often assumed, but many other options can be implemented in a Bayesian hierarchical framework. For instance, dispersal may be modelled using a longitude and a latitude component[26] or considering individual heterogeneity in dispersal behaviour[43].

The flexibility of Bayesian models is further illustrated by the possibility of mapping emigration probabilities in our study area (Fig. 4). The notable differences found among sexes and across space can provide a deep understanding of population and metapopulation dynamics to (1) illustrate the magnitude of the border effect and how it can differentially affect different fractions of a population; (2) reveal the heterogeneous contribution of territories to local population processes; and (3) understand whether unobserved individuals might be more likely attributable to either emigration or mortality. Such knowledge can be important to managers as often critical conservation decisions have to be made within short periods of time and with few up-to-date information[44].

Despite the generality and flexibility of our modelling approach, there may be situations where the joint estimation is not adequate. The present framework has been designed to model natal dispersal and subsequent permanent emigration, since in most animal species natal dispersal accounts for most-to-all long-distance dispersal movements in a population, and is by far the most important determinant of permanent emigration. This view is often considered the paradigm in animal populations[2,45]. However, the method does not account for breeding dispersal. This type of dispersal is commonly composed of short movements that mostly generate cases of not permanent but temporary emigration, which may mainly bias recapture probabilities and often has a more limited effect on other demographic parameters[17]. Nevertheless, there may be some species or populations in which breeding dispersal is similar or larger than natal dispersal. In such cases, breeding dispersal may (1) become a significant contributor to permanent emigration, and (2) frequently cause individuals that have moved outside the study area due to natal dispersal to come back to it. Both phenomena, if frequent, may have the capacity to bias the estimates provided by the joint estimation method, as there are sources of permanent emigration that are not accounted for, or on the contrary, permanent emigration may be confused with temporary emigration. Large breeding dispersal patterns appear to be related to specific ecological conditions rather than evolutionary or phylogenetic reasons[2]. In birds, this may be the case for populations with highly patchy distributions and very specific ecological requirements, like wetlands that may be poorly connected[46]. Thus, the present method should be used with caution when considerable permanent emigration caused by breeding dispersal is suspected, and other approaches may be more suitable (e.g.,[6,26,43]). One further limitation of the joint estimation approach may emerge in cases of study areas very restricted in size combined with populations with large natal dispersal capacities. In such cases, very few dispersal events may be detected, which may hamper the ability of joint estimation methods to provide consistent corrections in demographic parameters[26]. To address this issue, Bayesian models might provide a solution in the form of priors if direct or indirect information about dispersal exists[47]. In these situations, telemetry data could be a very useful source of dispersal information, if available. Other potential limitations of the joint estimation approach may arise from the fact that the method requires modelling territories or the distribution of the species inside, and especially outside the study area. In some species, the information about the distribution or number of territories can be poor. In these cases, modelling wrong territory distributions or numbers along space could push the estimates of dispersal and permanent emigration probabilities to be either underestimated or overestimated. These biases could propagate and lead to unrealistic estimations of true survival and other demographic parameters. Hence, a realistic modelling of the range, number, and/or distribution of territories appears important for an optimal performance of the method.

Overall, the joint estimation method presented here provides a promising framework to reduce biases in dispersal and survival estimates in mark-recapture analyses. In addition, this may be a useful formulation for future studies to assess additional sources of individual or population heterogeneity in dispersal and permanent emigration as well as their impacts in survival and other demographic parameters. Here, we show how the permanent emigration bias has different effects in the estimates of males and females. However, age, morphologic, and genetic traits may also affect individual permanent emigration probabilities[2,6,48,49]. Breeding density, nest occupation, and intraspecific competition in source and destination areas may also contribute to shaping natal dispersal, with higher densities or interactions often associated with larger dispersal patterns[15]. Including information on such processes (e.g., as covariates) in future joint-estimation-based studies may help disentangling the complexity of dispersal processes and their multiple population and evolutionary drivers using mark-recapture data.

Methods

General modelling approach. The joint estimation approach described here consists of a Bayesian hierarchical model structured in a multistate CMR submodel and a spatial submodel (Fig. 6). Both components must be linked by a parameter that informs the model about permanent emigration probabilities by means of estimating an individual's probability to permanently leave the study area conditional on its natal dispersal distance, in addition to mortality considerations. We use the spatial/dispersal information provided by this parameter to guide a state transition in the multistate CMR submodel, in which an individual may move from a live state at t to an absorbing state (a permanently unobservable state) at $t+1$ in case it leaves the study area. This transition is the key point of the joint estimation approach, as it allows the model to infer the true dispersal kernel and sub-

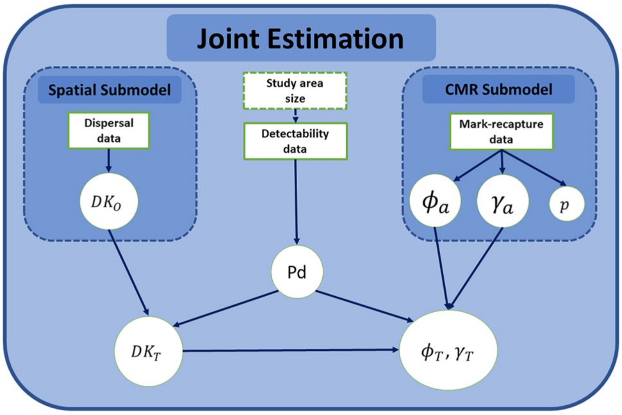

Figure 6. Diagram of the Joint Estimation framework. Data types are inside solid squares (study area size is inside a dashed square as study area information is implicitly provided by detectability data). Parameters are shown inside circles. Parameters DK_o and DK_T stand for the observed and the true dispersal kernel respectively. Parameters φ, γ, and *p* from the CMR submodel account for apparent survival, apparent recruitment, and recapture estimates. Parameter P_d provides information on detectability at different dispersal distances for every individual and links the spatial and the CMR submodels. Note that the absence of parameter P_d would lead to a separate (i.e., unlinked) estimation of survival and dispersal.

sequently address the biases in demographic parameters. We provide a detailed description of the mathematical, statistical, and modelling features of the joint estimation approach in the Methods section *Joint Estimation of natal dispersal kernel and detection probabilities*. This is a flexible formulation that can be applied to a wide range of species and ecological contexts. Overall, it is applicable to species in which natal dispersal is the main driver of permanent emigration and shows markedly larger distances than breeding dispersal, as is common in most wild populations[2]. In addition, study areas should not be very restricted in size, to the extent that breeding dispersal does not easily exceed its limits and thus contribute to permanent emigration along with natal dispersal.

As estimating natal dispersal is a central point of the method, it is essential that monitoring schemes focus on tagging individuals at birth sites and reencountering them as breeders. Since natal dispersal is intrinsically related to sexual maturity, the transition matrices of multistate CMR models should be adjusted to reflect the breeding biology of the study species (i.e., modelling maturity, or the age of first breeding as a fixed or varying age;[50]). Here, we adapted this formulation to the Bonelli's eagle study system, in which the study area was structured into territories. We modelled recruitment to a breeding territory as an equivalent to sexual maturation since individuals start showing territorial behaviour right after maturation. In addition, in our example, whenever an individual recruits to a non-monitored territory (i.e., outside the study area), it is counted as a permanent emigration case. We included dead recoveries to increase the precision of our estimates, but these are not necessary to implement this design (Appendix S3). Further insights on the applicability and potential shortcomings of this approach are developed in the Discussion section.

Study population and life cycle. The Bonelli's eagle is a territorial long-lived raptor with delayed maturity and low breeding rates whose range extends from south-east Asia to the western Mediterranean. Our focal population is located in Catalonia (NE Spain) and holds ca. 82 breeding pairs[51]. As in many other territorial raptors, the population is structured into the non-territorial (i.e., non-breeding) and territorial (i.e., breeding) fractions. After the post-fledging dependence period, individuals are non-territorial and show a transient nomadic behaviour with frequent visits to areas away from breeding territories[33]. Birds become territorial (i.e., breeders) after sexual maturity and recruitment to the breeding population, which mostly occur between three and four years of age[34]. As they establish in territories, birds start displaying territorial and pair-binding behaviour, with strong fidelity to their first breeding areas and very infrequent breeding dispersal[52]. Between breeding seasons, individuals either do not leave their territories or stay in their surroundings[33]. Given the strong link between sexual maturity, territoriality, and breeding in this species, we refer to (non)-territorial and (non)-breeding individuals as equivalent terms.

We used data from an intensive tagging and monitoring programme (2008–2020), where 461 chicks born in 51 different territories were ringed in their nests with metal and alphanumeric colour rings. All rings were riveted to avoid tag loss. To recontact tagged non-breeders, we monitored the two main dispersal areas away from breeding territories in Catalonia, which are located in Tarragona and the Lleida Plains. Dispersal areas are sites with large prey availabilities, which attract large amounts of non-breeders[33]. In addition, we monitored 76 different territories in our focal study area to detect breeding birds. For territory monitoring, we used both telescope observation routines and camera-trapping monitoring from January to May (breeding season). 178 marked individuals were recontacted alive, 83 of which were territorials (60 inside the study area, 23 outside). In addition, we recovered 75 dead marked individuals (62 non-breeders, 13 breeders) from the surveillance of territories, dispersal areas[33], and zones of high mortality risk (i.e., power infrastructures, ponds) by monitoring and ranger teams. Sexing was done by DNA analyses, biometry[53] and breeding behaviour assessments. Given the strong breeding site fidelity of territorial raptors, monitoring schemes usually prioritize breeding territories that were known to be occupied in previous years, while recruitments in unoccupied territories might become unnoticed. In addition, whenever a ringed individual is detected in a territory for the first time, monitoring teams usually put additional efforts in reading the rings from year to year. While this is a common monitoring strategy, it may generate heterogeneity between the first-time and subsequent detection probabilities of breeders. Hence, this source of breeder detection heterogeneity needs to be modelled accordingly to obtain unbiased demographic estimates[50].

The multistate CMR submodel. *Multistate modelling.* We modelled three different scenarios (SEP-CAT, JOINT-CAT and JOINT-ALL) under gamma and lognormal dispersal distributions. We used Bayesian multistate CMR designs to model survival, dispersal, and territory recruitment, along with recapture and recovery probabilities. Models were built and run in the BUGS language using the R package NIMBLE[54]. For the modelling of multistate transitions, we used the same state-transition matrices and age structures across models following the extensive knowledge about the demography of the species[55] to facilitate result comparisons among models. We chose vague priors for all but dispersal variables (i.e., Uniform (0,1) and Beta (1,1) for variables bounded between 0 and 1; Normal (0, sd = 1.5) for logit-transformed variables;[50,56]. See section *The Spatial Submodel* for information about dispersal priors. In addition, to avoid violation of the instantaneous sampling assumption, we pooled sampling occasions into 6-month periods: January to June, and July to December[10]. As in most Bayesian CMR models, we used a hierarchical state-space design with two components: first, the state process described by the state transition matrix, which defines how individuals change their biological states between consecutive capture occasions; and second, the observation process described by the observation matrix, which indicates how individual observations relate to the states of the individuals. Transitions among true states are represented by a matrix of latent states *z*, while information about observations is provided by the CMR matrix *y*. Transitions among states and associations between states and observations were modelled with a categorical distribution

$$z_{ind,time} \sim Categorical(ps[z_{ind,time-1}])$$

where *ps* is the matrix of transitions among states (Appendix S1, Figure S1), and

$$y_{ind,time} \sim Categorical(po[z_{ind,time}])$$

where *po* is the event matrix (Figure S2).

The state and observation processes. We defined five different states common to all models (Figure S1): (1) Alive Non-Breeder (ANB), (2) Alive Breeder (AB), (3) Dead as Non-Breeder (DNB), (4) Dead as Breeder (DB), and 5) the Absorbing State (AS). Note that there is one unobservable state in this definition: the Absorbing State (AS). The AS lacks a biological meaning but is used in multistate modelling to group all those individuals that enter a state that cannot be observed anymore throughout the course of the study. Transitions in the state matrix and relationships in the observation matrix were defined using parameters with different structures to match the biological and demographic features of the species (Fig. 7), which are described hereunder.

Survival, recruitment, and recovery. We modelled survival (φ) as time-constant but varying by sex and breeding status. Survival of breeders (φ_B) was modelled as constant. For JOINT-ALL models, we modelled φ_B as varying between inside and outside the study area since we incorporated observations of breeders from the whole range of the species,. Survival of non-breeders (φ_{NB}) was structured by age classes to accommodate typical age-related variation in long-lived populations and to be able to assess which population fractions were most affected by permanent emigration. Specifically, non-breeder survival was estimated separately for juveniles (1yo), immatures and subadults (2–3 yo) and adults (>= 4 yo), following Hernández-Matías et al.[52]. Sexual maturity was modelled as the probability of joining the breeding population, that is, occupying a breeding territory, so-called "recruitment" (γ). Recruitment was modelled as a sex and age-varying probability for juveniles (1yo), immatures (2yo), subadults (3yo) and adults (>= 4yo) (see[34]). The recovery parameter (r) was defined as the probability of encountering a dead marked individual. We modelled it as time-constant, but different for breeders (r_B) and non-breeders (r_{NB}) to accommodate any variation that may arise from differences in mortality causes associated with differences in behaviour and risk exposure. While recovery has traditionally been modelled in the observation matrix, we modelled it in the state transition matrix to avoid reported convergence issues in Bayesian hierarchical models[50].

Recapture parameters. Recapture probabilities (i.e., probability of observing a live tagged individual) were modelled differently for non-breeders and breeders. Recapture of non-breeders (P_{NB}) was modelled as constant across sex, time, and age classes. In addition, to accommodate the effects of breeder detection heterogeneity, we divided recapture probabilities of breeders into two parameters: 1) P_{B1}: the probability of observing a ringed breeder for the first time, and 2) P_B: the probability of observing it in subsequent occasions once it was observed for the first time[50]. Since breeders are only monitored during the breeding season, which occurs entirely during the first half of the year (i.e., January to June), P_B and P_{B1} were set as 0 at the second halves of the years (i.e., July to December). P_{B1} varied by territory of recruitment of each individual and time (see details about its estimation below in this section), and P_B varied by year using random effects to accommodate variations in territory sampling effort. In JOINT-ALL models, since we incorporated observations of all the distribution range, we differentiated P_B between Catalonia (yearly variation, random effects) and outside (constant probability).

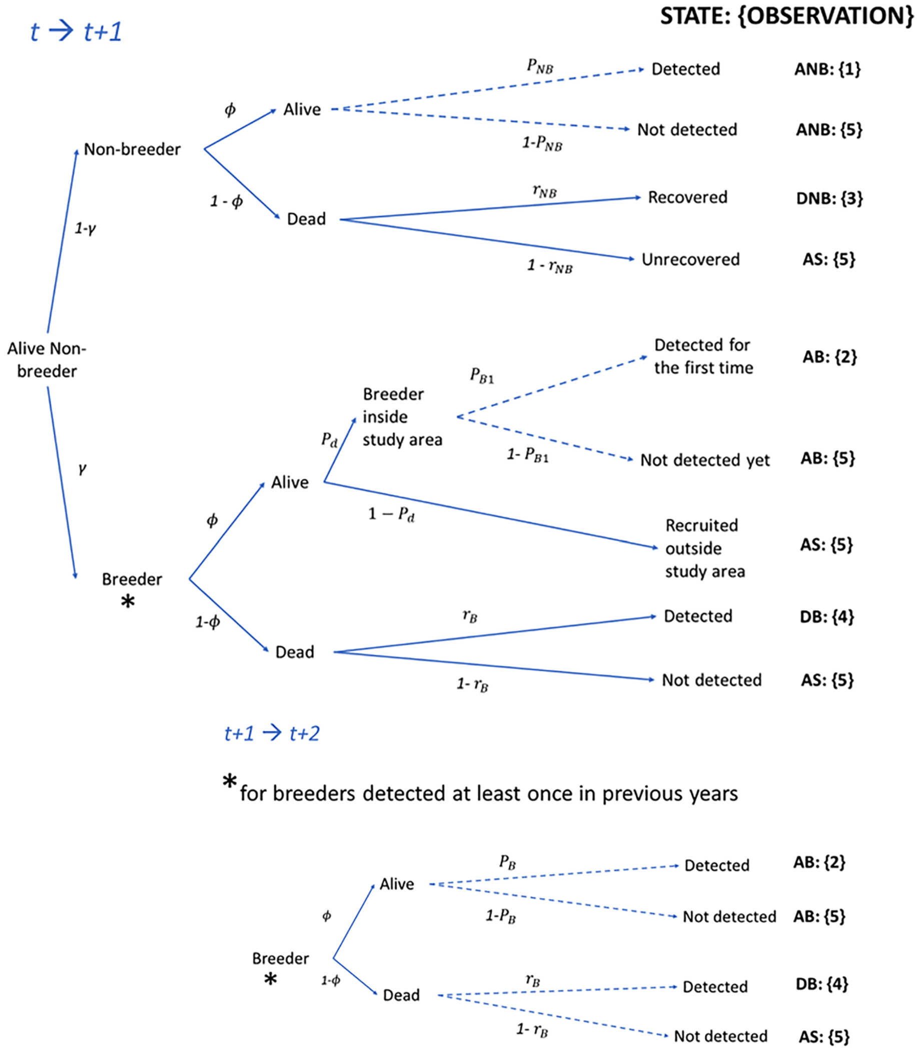

Figure 7. Graphical representation of state transitions, observations, and parameters from occasion *t* to *t + 1* for an individual ringed at birth. Solid lines indicate transitions in the state matrix and dashed lines indicate transitions in the observation matrix. State codes are ANB (Alive Non-Breeder), AB (Alive Breeder), DNB (Dead Non-Breeder), DB (Dead Breeder) and AS (Absorbing State). Numbers in brackets ({}) indicate corresponding codes in the observation matrix columns and encounter histories. Parameter symbols stand for survival (ϕ), recruitment (γ), recapture (P_B and P_{NB}), recovery (*r*) and the first-encounter breeder recapture parameter (P_{B1}). *In the lower diagram, transitions of breeding individuals from *t + 1* to *t + 2* are shown. Because of the implementation of breeder recapture heterogeneity, individuals that become breeders at t + 1 may or may not be observed for the first time depending on probability P_{B1}. Once individuals are first observed, the observation probability P_B is implemented at subsequent occasions.

The division of breeder recapture probabilities between P_B and P_{B1} was made because, given the system of monitoring implemented in the study area, monitoring teams would put more efforts into recontacting tagged breeders that had been observed previously in a certain territory. This fact would generally make newly recruited tagged birds less likely to be observed for the first time. This detection heterogeneity was represented using a parameterisation into the observation matrix that incorporated an individual and time-varying binary covariate $covpb_{i,t}$ along with P_B and P_{B1} to model the breeder observation process (Fig. 7; Figures S1, S2).

$$P(Observed\ as\ AB|State\ AB)_{i,t} = \left(PB1_{terr_i,t} * \left(1 - covpb_{i,t}\right)\right) + \left(P_{B_t} * covpb_{i,t}\right)$$

For every individual, $covpb_{i,t}$ would take value 0 before and at the occasion of first detection of a breeder, and 1 at subsequent occasions. Hence, when $covpb_{i,t}= 0$, first-time breeder recapture probability P_{B1} was used to model the observation process conditional on the individual having recruited as a breeder but not yet observed, or observed for the first time. Instead, when $covpb_{i,t}= 1$ (i.e., all along after first breeder detection), P_B was applied. In cases where an individual was never observed as a live breeder, *covpb* consisted of a row of zeros.

Importantly, P_{B1} may be poorly estimable from CMR data alone, as it refers to a single observation phenomenon (i.e., the first observation of a recruit), and thus to estimate it we used additional data. In our study system, each territory was routinely monitored every breeding season using either (1) telescope watching routines, (2) camera-trapping, or (3) a combination of both methods. All three methods followed standardized protocols in terms of the number of monitoring days per territory and breeding season, so that the observation effort was similar across territories and breeding seasons for each method. The chances of detecting a ringed breeder for the first time basically depend on the effectiveness at detecting ringed birds of the specific monitoring routine used in a territory during the breeding season. During monitoring routines, birds are searched inside territories by either of the three methods to try to ascertain whether they wear alphanumeric rings. If they do, additional efforts are carried out to read the alphanumeric codes in order to individually identify every breeder. Hence, to estimate P_{B1}, we modelled information written down during the 2008–2020 monitoring surveys about the success/failure at distinguishing with certainty whether or not a breeding individual wore an alphanumeric ring in their tarsus when a territory surveillance season was performed with either telescopes, camera-traps, or both methods altogether. We assumed that the probability to first detect a ringed breeder was equal to the probability of distinguishing with certainty if it wore an alphanumeric ring, as in all cases rings were read after noticing that they were present in new breeders. We analysed these data with a logistic regression using ascertained ring presence/absence in an individual during a breeding season (*plr_i)* as a response variable indicating (0): ring presence/absence could not be ascertained, and (1): ring presence/absence was ascertained. We used the monitoring methods as explanatory variables (*obs* for territory monitored using telescope routines and *camtrap* for camera trapping monitoring routines) indicating (1): method used, and (0): method not used.

$$logit\left(plr_i\right) = \alpha + \beta_1 * obs_{terr\,i} + \beta_2 * camtrap_{terr\,i}$$

The resulting estimates of effectiveness of each method were assigned to each territory depending on the type of monitoring used at each. Hence, P_{B1} would take a different value for each breeder depending on their territory of recruitment. In total, 55 (72%) territories were monitored with telescope routines only, 7 (9%) territories with camera trapping only, and 14 (19%) territories with both methods.

In SEP-CAT and JOINT-CAT models, the types of monitoring used in all territories were known with certainty. Since we aimed to reproduce a scenario without monitoring information outside our focal area, all territories outside Catalonia were assigned as unmonitored. Instead, when fitting the JOINT-ALL models, we did not have complete information about which specific territories were unmonitored or monitored, or by which method, in order to implement P_{B1}. Therefore, we made reasonable modelling assumptions to reproduce the real conditions of monitoring. First, we assigned as monitored by any method or unmonitored those territories we had information about (n = 106, 30 of which outside the study area). In addition, we obtained information about the percentage of monitored territories and the frequency of usage of each method in each monitored population in Western Europe from Hernández-Matías et al.[3] and updated unpublished information. We dealt with this uncertainty by modelling the monitoring status of each territory by each method as a Bernoulli-distributed variable with a probability equal to the percentage of monitored territories per region:

$$obs_{terr} \sim Bernoulli(\%obs\left[region_{terr}\right])$$

$$camtrap_{terr} \sim Bernoulli(\%camtrap\left[region_{terr}\right])$$

where *region* stands for each of the different regions with Bonelli's eagles present in western Europe and *terr* stands for each territory included in the models.

The spatial submodel. *Territories and natal dispersal.* The distribution of breeding territories in Western Europe was represented as a point process, where each point corresponds to the location of a Bonelli's eagle nest occupied during this study. Note that due to the strong fidelity of the study species to territories and nesting sites, territory and even nest locations rarely vary from year to year, which allow the definition of a territory as a static point[52]. Exact coordinates of breeding territories were available for all territories in the study population (i.e., Catalonia, n = 76) as well as for populations in Portugal (n = 93) and France (n = 44). For the rest of populations, all of them in Spain, territory locations were not known with certainty, and thus were simulated using updated data about the distribution and number of territories in different regions[51]. First, we used 10 × 10 km presence/absence grid data for the species in Spain[51] and smoothed the data into a distribution map assuming territories would be circular with a 7-km radius (value obtained from radiotracking data). Then, following Atlas data on the number of territories per Spanish province for the same period[51], we simulated territory locations inside the distribution areas of the species in every province, assuming a minimum distance between territories of 2 km. In total, 702 territory locations were simulated, which adds up to a total of 916 territories considered in this study (Figure S3).

Natal dispersal was measured as the geodesic distance between the territories of birth and recruitment. The territories of birth of all individuals were known with certainty as all birds were ringed as chicks. We modelled natal dispersal as different by sex, since raw data suggested that females tended to disperse further away[31,34]. Dispersal was modelled under the assumption of isotropical conditions (i.e., dispersal direction was uniform along the distribution range of the species), and therefore dispersal distributions needed to be strictly positive. The isotropical modelling was chosen due to the large numbers of territories available along the distance in the western European range of the species and the observed large dispersal capacity of the species in relation to the distance between birth and potential recruitment territories (Figure S4), which may help avoiding inconsistencies when using this modelling approach. We chose both a gamma and a lognormal distribution as dispersal kernel candidate functions. The gamma distribution was chosen due to its flexibility in modelling from exponential dispersal patterns to right-skewed kernels showing relatively high dispersal probabilities at large distances. The lognormal distribution was selected to represent right-skewed, fat-tailed dispersal kernels with higher dispersal probabilities at large distances. Both distributions were truncated at 1200 km because (1) no birds have ever been observed beyond that distance from a birth site (own data), and (2) this goes slightly far beyond the maximum distance between birth territories in the study area and other territories in SW Europe (ca. 1180 km). As for dispersal priors, we chose weakly informative priors that provided practically identical prior distance expectations for both distributions. We based our prior choices on published literature on natal dispersal in this species[34]. We performed prior predictive checks to ensure priors on distribution parameters were providing very similar and realistic prior dispersal distances[57,58]. In addition, we compared our final prior choices to alternative prior sets, and we checked that the sensitivity of our models' posterior inferences to different prior choices was robust[57,58]. Our prior selection and analysis workflow for dispersal parameters is described in detail at Appendix S4 and Figures S12–S16 therein. To represent territorial recruitment, we provided *DM*: a 51 × 916 matrix with geodesic distances between all territories where chicks had ever been ringed during the study period (n = 51) and potential territories of recruitment (n = 916: 76 in Catalonia, 840 outside). We modelled natal dispersal distances for every individual as random draws from the sex-specific dispersal kernels. Next, we compared every individual's drawn distance to the whole set of distances between the individual's territory of birth and potential territories of recruitment provided in *DM*, and we assigned each recruit to the territory that showed the closest value to the drawn distance.

Joint estimation of natal dispersal kernel and detection probabilities. The complexity of the permanent emigration challenge stems from the interplay between detection and dispersal probabilities[23,25]. Essentially, the observed natal dispersal kernel from a marked population in a study area restricted in size (DK_o) is the result of the interaction between the true natal dispersal kernel (DK_T) and the probability that natal dispersal events end up inside the study area (W) conditional on the location of departure of every dispersal movement (territory of birth in this case) and dispersal distance: $DK_o = DK_t * W$. The smaller the study area is, the greater the probability that a dispersal event will end up outside the boundaries of a study area and thus be indetectable, which may increase the difference between DK_o and DK_t. Hence, the joint estimation formulation focuses on addressing this interplay. To do so, we first inform the model about which territories are inside or outside the study area. We do this with the binary vector *rp*, which indicates whether each of all 916 territories modelled in our study is (1) monitored (i.e., inside the study area), or (0) unmonitored (i.e., outside). We simulate natal dispersal distances for every individual as random draws from the kernel distribution and assign each breeder to a territory using the distance information provided by matrix *DM*. Next, we generate the binary vector P_d, which using the information provided by *rp*, stores whether the territory of recruitment of each individual is (1) monitored/inside the study area, or (0) unmonitored/outside. Hence, P_d contains the information about every individual's likelihood to remain or leave the study area (W), which is the key to estimate the true dispersal kernel DK_T. Importantly, since P_d is individual-specific, it accounts for the fact that individuals will be more or less likely to remain in the study area after natal dispersal depending on their area of birth (i.e., the border effect). To act as a link between the spatial and the CMR submodels, P_d is incorporated into the state transition matrices in JOINT models (Figs. 6, S1). There, P_d is included to the transition from t to $t+1$ for each individual i from state *Alive Non Breeder* to either *Alive Breeder* (i.e., breeder and inside the study area, thus detectable) if $P_d = 1$, or the *Absorbing State* (i.e., breeder and outside the study area, thus permanently undetectable) if $P_d = 0$, conditional on survival and recruitment. The Absorbing State (AS) retains all those individuals that enter a permanently unobservable state (see in the state matrix, Appendix S1, that the probability of transitioning from AS at t to AS at $t+1$ equals 1). Traditionally, the AS has been used to indicate that dead individuals will remain dead and unobservable forever. Modelling-wise, the permanent emigration process is equivalent to mortality, as individuals that have left the study area will remain unobservable forever[32]. Hence, by modelling permanent emigration as a transition to the AS, whenever a non-breeder is not observed anymore throughout the course of the study, the model estimates the chances of it (1) being alive in the study area while remaining undetected, (2) having permanently emigrated from the study area, conditional to its natal dispersal distance, and (3) being dead and unrecovered. This approach allows the model to estimate the true dispersal kernel while dealing with the uncertainty present in the system (Fig. 6).

Mapping permanent emigration by sex, territory, and distribution area. Based on the dispersal kernels by sex provided by the models, we performed simulations to estimate and map the continuous probability of permanent emigration by territory and sex. Simulations allowed us to make both males and females be born homogeneously across all territories in the study area (n = 76). To model natal dispersal, we used the sex-specific lognormal dispersal kernel estimates and their associated uncertainties obtained at JOINT-ALL. We built a model simulating natal dispersal events from males and females from each territory following the same st ructure as in the rest of models: natal dispersal distances were simulated as random draws from kernel distributions, recruitment was simulated following the distance information from matrix *DM*, and we again made use of vector *rp* to indicate whether each territory of recruitment was either inside or outside the study area. Territory-specific permanent emigration probabilities were calculated as the probabilities of recruiting outside the study area from each birth territory. Next, we mapped these space-discrete (i.e., territory-specific) probabilities and used a Gaussian process regression (spatial kriging) for interpolation[59] to represent permanent emigration as a continuous probability along the distribution area of the study population. Interpolation was performed with ArcGIS Pro 2.5.2[60].

Model implementation. We checked for any deviations from the main assumptions of multistate models using Jolly-Movement (JMV) goodness-of-fit tests in software U-CARE 2.3.4[61]. As for Bayesian models, Gamma models (i.e., SEP-CAT-Gamma, JOINT-CAT-Gamma and JOINT-ALL-Gamma) were run for 4 chains of 70,000 iterations each, of which the first 50,000 were discarded. Lognormal models were run for 4 chains of 120,000 iterations each, and we discarded the first 100,000. Simulations to map permanent emigration probabilities were run for 4 chains of 100,000 iterations, of which the first 80,000 were discarded. All models were run in NIMBLE 0.12.1[54] and R 4.1.2. Results are presented as medians followed by 89% Highest Posterior Density Intervals (HPDI[56]) in brackets.

Data availability

The code used during the current study is available in the figshare repository, https://figshare.com/s/ec4e606c21f774c8cf43. The datasets analysed during the current study are available in the same figshare repository upon publication date.

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Author contributions

A.H-M., J.R., and J.A.B-B. conceived the central ideas of the manuscript. F.P., J.B., J.R., and A.H-M designed data collection, and collected the data. F.P., J.B., J.R., A.H-M, and J.A.B-B cleaned, wrangled, and formatted the data. J.A.B-B, A.H-M, J.L.R., and F.B. provided insights into the modelling framework and methods to use. J.A.B-B built the models and analysed the data. J.A.B-B and J.L.R. designed and prepared the figures. All authors contributed to the interpretation and writing of the results. J.A.B.-B., A.H.-M., J.L.R., F.B., and J.R. wrote the rest of the manuscript. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to J.A.B.-B.

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Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses

Badia-Boher, J.A., Real, J., Riera, J.L., Bartumeus F., Parés, F., Bas, J.M., & Hernández-Matías, A.

Appendix S1: Multistate submodel - state and observation matrices

$$
\begin{array}{c|c}
t/t+1 & \begin{array}{ccccc} \textbf{ANB} & \textbf{AB} & \textbf{DNB} & \textbf{DB} & \textbf{AS} \end{array} \\
\begin{array}{c} \textbf{ANB} \\ \textbf{AB} \\ \textbf{DNB} \\ \textbf{DB} \\ \textbf{AS} \end{array} &
\begin{bmatrix}
(S_{NB_{a,s}} * (1-\gamma_{a,s})) & (S_{NB_{a,s}} * \gamma_{a,s} * P_{d_i}) & (1-S_{NB_{a,s}}) * (1-\gamma_{a,s}) * r_{NB} & (1-S_{NB_{a,s}}) * \gamma_{a,s} * r_B & *_A \\
0 & S_{B_s} & 0 & (1-S_{B_s}) * r_B & (1-S_{B_s}) * (1-r_B) \\
0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 1
\end{bmatrix}
\end{array}
$$

$$*\mathrm{A}: \left((1-S_{NB_{a,s}}) * (1-\gamma_{a,s}) * (1-r_{NB})\right) + \left(S_{NB_{a,s}} * \gamma_{a,s} * (1-P_{d_i})\right) + \left((1-S_{NB_{a,s}}) * \gamma_{a,s} * (1-P_{d_i})\right) + ((1-S_{NB_{a,s}}) * \gamma_{a,s} * (1-r_B) * P_{d_i})$$

Figure S1. State transition matrix of the multistate joint-estimation models. Rows indicate state of individual i at time t, columns indicate state of individual i at time t+1. The matrix includes the parameters S_{NB} (non-breeder survival), S_B (breeder survival), γ (recruitment to the breeding population), P_d (joint-estimation parameter), and r (probability of encountering a dead marked individual that was either non-breeder, r_{NB}, or breeder, r_B). Subindices indicate age ($_a$), individual ($_i$), time ($_t$), and sex ($_s$). States are Alive as Non-Breeder (ANB), Alive as Breeder (AB), Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Due to the length of the first absorbing state expression (i.e., transition from ANB in t to AS in t+1), we wrote this expression outside the matrix ($*_A$).

$$
\begin{array}{c|c}
t/t & \begin{array}{ccccc} \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} \end{array} \\
\begin{array}{c} \textbf{ANB} \\ \textbf{AB} \\ \textbf{DNB} \\ \textbf{DB} \\ \textbf{AS} \end{array} &
\begin{bmatrix}
p_{NB} & 0 & 0 & 0 & 1-p_{NB} \\
0 & p_{B1_{terr_i,t}} * (1-covpb_{i,t}) + p_{B_t} * covpb_{i,t} & 0 & 0 & 1-p_B \\
0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 1
\end{bmatrix}
\end{array}
$$

Figure S2. Observation matrix of the multistate joint-estimation models. Rows indicate states of individual i at time t, columns indicate observationa/eventa of individual i at time t. The matrix includes the parameters p_{NB} (non-breeder recapture), p_{B1} (probability of being observed for the first time once the individual has become breeder), and P_B (breeder recapture for those individuals observed as breeders at least once already), and the binary covariate covpb, which assigns either PB1 or PB as observation parameters to deal with detection heterogeneity in breeder detection probabilities. Subindex ($_{terr}$) stands for "territory". States are Alive as Non-Breeder (ANB), Alive as Breeder, Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Observations/Events are Alive as Non-Breeder (1), Alive as Breeder (2), Recovered as Non-Breeder (3), Recovered as Breeder (4) and Unobserved (5).

Appendix S2: Supplementary figures and tables of Methods and Results

Table S1. Main survival and average dispersal distance results by model.

Estimate	Age	Sex	Distribution	Model estimates: Median (89%HPDI)		
				Sep-Cat	**Joint-Cat**	**Joint-All**
Avg. Disp. Distance (km)	(all)	Female	Gamma	95.2 (65.3 – 123.6)	114.7 (72.4 – 155.8)	159.6 (121.2 – 194.7)
			Lognormal	124.7 (77.1 – 173.0)	221.0 (92.1 – 336.2)	213.6 (126.6 - 289.6)
	(all)	Male	Gamma	35.6 (27.9 - 43.1)	37.0 (28.8 – 45.9)	71.1 (51.1 – 89.9)
			Lognormal	46.5 (32.6 - 59.1)	52.8 (35.0 – 75.5)	73.3 (47.1 – 97.2)
Non-Breeding Survival	1 yo.	Female	Gamma	0.626 (0.529 - 0.725)	0.645 (0.546 - 0.747)	0.677 (0.588 - 0.770)
			Lognormal	0.627 (0.533 - 0.731)	0.667 (0.568 - 0.768)	0.674 (0.580 - 0.764)
	2-3 yo.	Female	Gamma	0.622 (0.522 - 0.720)	0.658 (0.553 - 0.761)	0.706 (0.618 - 0.788)
			Lognormal	0.626 (0.524 - 0.722)	0.684 (0.578 – 0.782)	0.701 (0.613 - 0.785)
	Adults	Female	Gamma	0.820 (0.645 - 0.979)	0.846 (0.681 - 0.992)	0.897 (0.781 - 0.990)
			Lognormal	0.818 (0.642 - 0.976)	0.857 (0.695 - 0.996)	0.892 (0.775 - 0.991)
	1 yo.	Male	Gamma	0.611 (0.509 - 0.711)	0.622 (0.523 - 0.723)	0.648 (0.555 - 0.742)
			Lognormal	0.621 (0.521 - 0.723)	0.641 (0.543 - 0.743)	0.644 (0.551 - 0.745)
	2-3 yo.	Male	Gamma	0.736 (0.644 - 0.828)	0.743 (0.652 - 0.832)	0.760 (0.671 - 0.844)
			Lognormal	0.739 (0.645 - 0.828)	0.759 (0.671 - 0.848)	0.758 (0.666 - 0.841)
	Adults	Male	Gamma	0.837 (0.717 - 0.947)	0.845 (0.721 - 0.948)	0.848 (0.735 - 0.952)
			Lognormal	0.839 (0.719 - 0.942)	0.846 (0.734 - 0.954)	0.848 (0.727 - 0.954)
Territorial Survival	(all)	Female	Gamma	0.879 (0.809 - 0.948)	0.874 (0.801 - 0.941)	0.870 (0.792 - 0.951)
			Lognormal	0.877 (0.805 - 0.944)	0.876 (0.801 - 0.942)	0.872 (0.800 - 0.940)
	(all)	Male	Gamma	0.886 (0.838 - 0.933)	0.887 (0.839 - 0.934)	0.886 (0.841 - 0.931)
			Lognormal	0.886 (0.834 - 0.932)	0.888 (0.838 - 0.934)	0.890 (0.845 - 0.937)

Table S2. Long-distance natal dispersal probability (i.e., distances higher than 200 km) by dispersal kernel and sex.

Sex	Distribution	Model estimates: Median (89%HPDI)		
		Sep-Cat	**Joint-Cat**	**Joint-All**
Female	Gamma	0.074 (0.006 – 0.165)	0.123 (0.017 – 0.271)	0.279 (0.178 – 0.385)
	Lognormal	0.143 (0.041 – 0.261)	0.288 (0.108 – 0.477)	0.306 (0.184 – 0.434)
Male	Gamma	0 (0 - 0)	0 (0 - 0)	0.054 (0.013 – 0.104)
	Lognormal	0.018 (0 – 0.045)	0.037 (0.002 – 0.102)	0.082 (0.028 – 0.151)

Table S3. Dispersal parameter estimates (i.e., shape and rate for gamma distributions, mean and standard deviation for lognormal distributions) by model type and sex.

Sex	Distribution	Parameter	Model estimates: Median (89%HPDI)		
			Sep-Cat	**Joint-Cat**	**Joint-All**
Female	Gamma	Shape	1.845 (1.205 – 2.547)	1.842 (1.166 – 2.534)	1.574 (1.123 – 2.035)
		Rate	0.020 (0.009 – 0.030)	0.017 (0.007 – 0.027)	0.010 (0.006 – 0.014)
	Lognormal	Mean	4.284 (3.951 – 4.644)	4.683 (4.213 – 5.249)	4.755 (4.412 – 5.098)
		sd	0.958 (0.729 – 1.203)	1.104 (0.804 – 1.421)	1.082 (0.859 – 1.332)
Male	Gamma	Shape	1.892 (1.325 – 2.509)	1.915 (1.321 – 2.543)	1.032 (0.752 – 1.311)
		Rate	0.054 (0.032 – 0.077)	0.052 (0.031 – 0.075)	0.015 (0.009 – 0.021)
	Lognormal	Mean	3.341 (3.084 – 3.605)	3.484 (3.164 – 3.848)	3.662 (3.366 – 3.971)
		sd	0.941 (0.758 – 1.134)	1.019 (0.778 – 1.269)	1.177 (0.965 – 1.424)

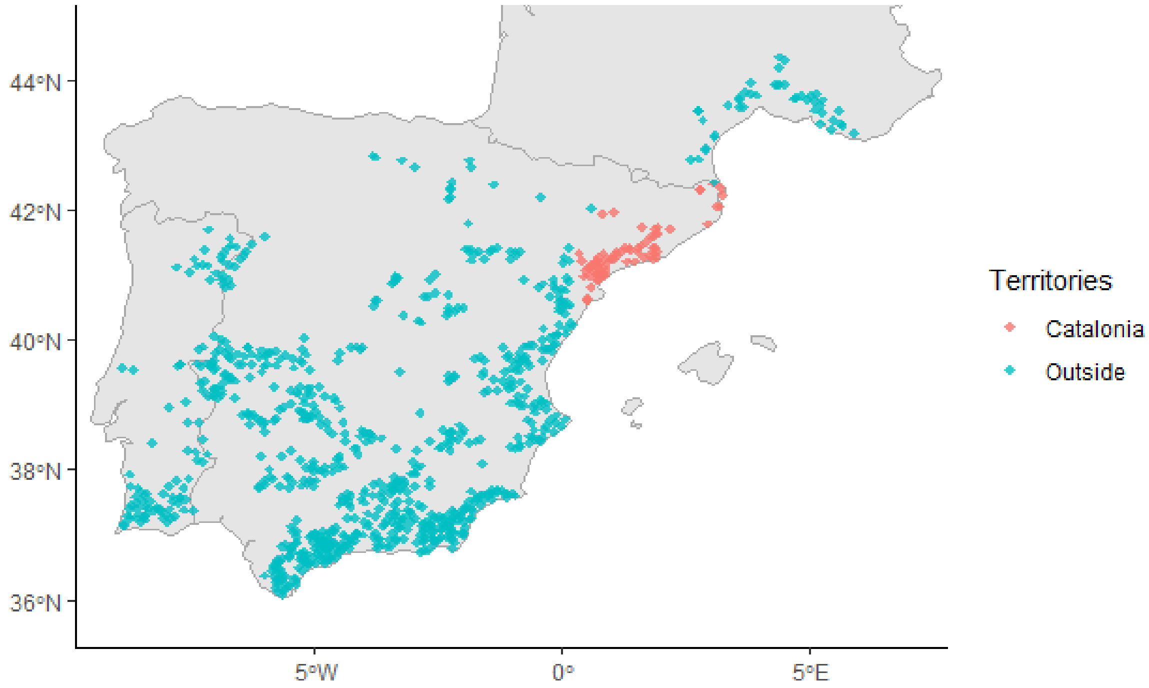

Figure S3. Locations of Bonelli's eagle territories in continental western Europe used in the spatial component of the models. Map source: Natural Earth

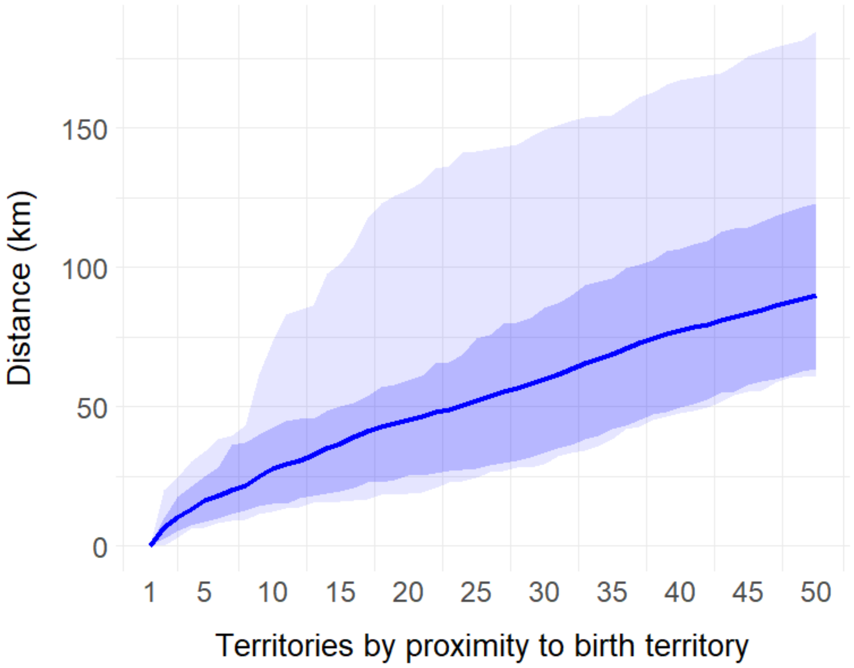

Figure S4. Mean (thick line), 85% quantile (strong blue shaded area), and 95% quantile (light blue shaded area) distance values between territories of birth and the 50 closest potential territories of recruitment.

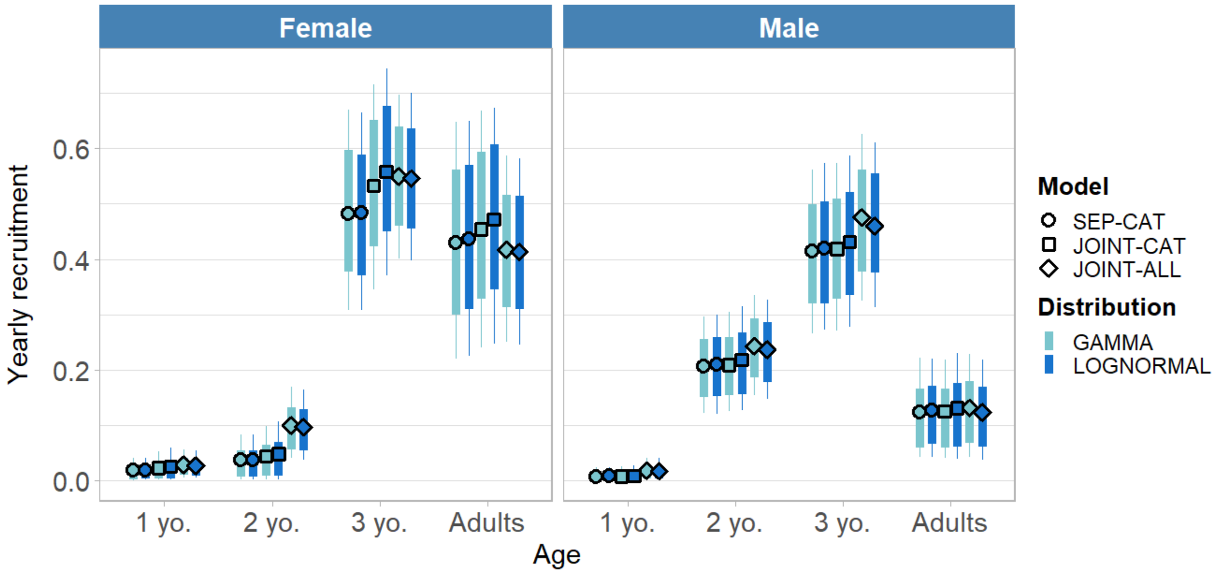

Figure S5. Recruitment probabilities by model, sex, and age. Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

Appendix S3: A brief guide on adapting the Joint Estimation multistate matrices to different study systems

The joint estimation approach is a flexible formulation to address biases in demographic parameters caused by permanent emigration. This model formulation is divided into a spatial submodel and a multistate capture-mark-recapture (CMR) submodel. The spatial submodel models natal dispersal, while the CMR submodel provides information on demographic parameters such as survival and sexual maturity (i.e., age of first breeding or recruitment to the breeding population, among other possibilities). Both submodels are linked by a specific parameter that estimates individual probabilities of permanent emigration accounting for information provided by both submodels and detectability along space. This parameter is accommodated in the state matrices of the multistate submodel to represent the permanent emigration process. Whenever an individual achieves sexual maturity, it undertakes natal dispersal towards the area of breeding. If that site is outside the study area, this is considered as permanent emigration. Such process is modelled as a transition to the absorbing state (i.e., a state of permanent undetectability) as the individual at issue will not be observable anymore throughout the course of the study. Based on this modelling approach, to implement the joint estimation it is only necessary to model survival and sexual maturity in the state matrix of the multistate submodel (Figure S6). As for the observation matrix, a single recapture probability would be necessary, same for breeders and non-breeders (Figure S7). Note that except for the pD parameter, which should be structured by individual in case we want to account for birth territory locations and the border effect, structuring parameters by age, sex, or sexual maturity status as in our study, is not necessary either for implementing this method.

$$\begin{array}{cc}
t\,/\,t^{+1} & \begin{array}{ccc} \textbf{ANB} & \textbf{AB} & \textbf{AS} \end{array} \\
\begin{array}{c} \textbf{ANB} \\ \textbf{AB} \\ \textbf{AS} \end{array} & \left[\begin{array}{ccc}
\left(S*(1-\gamma)\right) & \left(S*\gamma*P_{d_i}\right) & \left((1-S)+\left(S*\gamma*\left(1-P_{d_i}\right)\right)\right) \\
0 & S & 1-S \\
0 & 0 & 1
\end{array}\right]
\end{array}$$

Figure S6. Simplest state matrix possible to implement the joint estimation approach. States ANB, AB and AS stand for Alive – Non Breeder, Alive – Breeder and Absorbing State respectively. Parameters are S (survival), γ (sexual maturity / recruitment), and the individual-specific permanent emigration parameter P_d.

$$\begin{array}{c|c}
t\,/\,t{+}1 & \begin{array}{ccc} 1 & 2 & 3 \end{array} \\
\begin{array}{c} \text{ANB} \\ \text{AB} \\ \text{AS} \end{array} & \begin{bmatrix} P & 0 & 1-P \\ 0 & P & 1-P \\ 0 & 0 & 1 \end{bmatrix}
\end{array}$$

Figure S7. Simplest observation matrix possible to implement the joint estimation approach. States ANB, AB and AS stand for Alive – Non Breeder, Alive – Breeder and Absorbing State respectively, while observation codes 1, 2, 3 stand for Observed as Alive – Non Breeder, Observed as Alive –Breeder and Unobserved respectively. Parameter P stands for recapture probability.

The flexibility of the multistate capture-mark-recapture method may facilitate the adaptation of the joint estimation approach to other study designs. For instance, note that in Figure S6 we modelled the non-breeder to breeder transition as a stochastic probability, but if individuals become sexually mature at a fixed age (i.e., deterministically), this may also be adapted in the matrices using age states. As an example of an appropriate formulation, if an individual becomes sexually mature at the end of its second year of life, one may use the states "Alive – Non Breeder 1 year old", "Alive – Non Breeder 2 years old", "Alive – Breeder", and the Absorbing State (Figures S8 and S9). In this case, transitions from live states should only be determined by survival, as the probability to transition from being non-breeder at year 1 to being non-breeder at year 2, and to being breeder at year 3, only depends on surviving from year to year.

$$\begin{array}{c|cccc}
t\,/\,t{+}1 & \text{ANB 1Y} & \text{ANB 2Y} & \text{AB} & \text{AS} \\
\text{ANB-1Y} & 0 & S & 0 & 1-S \\
\text{ANB-2Y} & 0 & 0 & S * P_{d_i} & (1-S) + \left(S * \left(1 - P_{d_i}\right)\right) \\
\text{AB} & 0 & 0 & S & 1-S \\
\text{AS} & 0 & 0 & 0 & 1
\end{array}$$

Figure S8. State matrix adapting the multistate and joint estimation formulation to a species with a deterministic age of sexual maturity (at the end of the second year of life). States ANB – 1Y, ANB – 2Y, AB, and AS stand for Alive – Non Breeder at year 1, Alive – Non Breeder at year 2, Alive – Breeder, and Absorbing State respectively. Parameters are S (survival), and the individual-specific permanent emigration parameter P_d.

$$\begin{array}{c|cccc} t / t+1 & 1 & 2 & 3 & 4 \\ \hline \text{ANB-1Y} & P & 0 & 0 & 1-P \\ \text{ANB-2Y} & 0 & P & 0 & 1-P \\ \text{AB} & 0 & 0 & P & 1-P \\ \text{AS} & 0 & 0 & 0 & 1 \end{array}$$

Figure S9. Observation matrix adapting the multistate and joint estimation formulation to a species with a deterministic age of sexual maturity (at the end of the second year of life). States ANB – 1Y, ANB – 2Y, AB, and AS stand for Alive – Non Breeder at year 1, Alive – Non Breeder at year 2, Alive – Breeder, and Absorbing State respectively. Observation codes 1, 2, 3, and 4 stand for Observed at Alive – Non Breeder at year 1, Observed a Alive – Non Breeder at year 2, Observed as Alive – Breeder, and Unobserved respectively. Parameter P stands for recapture probability.

From these basic models, it is easy to add complexity to the state transition and observation matrices in further steps. For instance, from the simplest matrices presented here (Figures S6 and S7), we may add the modelling of recoveries of dead individuals (Figures S10 and S11. Recall that while recoveries have traditionally been modelled as observation parameters, in Bayesian hierarchical models and BUGS language we usually model them in the state matrices to avoid convergence issues.

$$\begin{array}{c|cccc} t / t+1 & \text{ANB} & \text{AB} & \text{D} & \text{AS} \\ \hline \text{ANB} & (S * (1-\gamma)) & (S * \gamma * P_{d_i}) & (1-S) * r & ((1-S) * (1-r)) + (S * \gamma * (1-P_{d_i})) \\ \text{AB} & 0 & S & (1-S) * r & (1-S) * (1-r) \\ \text{D} & 0 & 0 & 0 & 1 \\ \text{AS} & 0 & 0 & 0 & 1 \end{array}$$

Figure S10. State matrix adapting the multistate and joint estimation formulation to a study design with recoveries of dead individuals. States ANB, AB, D, and AS stand for Alive – Non Breeder, Alive – Breeder, (Recently) Dead, and Absorbing State. Parameters are S (survival), γ (sexual maturity), r (recovery), and the individual-specific permanent emigration parameter Pd.

$$\begin{array}{c|cccc} t / t+1 & 1 & 2 & 3 & 4 \\ \hline \text{ANB} & P & 0 & 0 & 1-P \\ \text{AB} & 0 & P & 0 & 1-P \\ \text{D} & 0 & 0 & 1 & 0 \\ \text{AS} & 0 & 0 & 0 & 1 \end{array}$$

Figure S11. Observation matrix adapting the multistate and joint estimation formulation to a study design with recoveries of dead individuals. States ANB, AB, D, and AS stand for Alive – Non Breeder, Alive – Breeder, (Recently) Dead, and Absorbing State respectively. Observation codes 1, 2, 3, and 4 stand for Observed as Alive – Non Breeder, Observed as Alive – Breeder, Observed as (Recently) Dead, and Unobserved respectively. Parameter P stands for recapture probability.

As shown, using the flexibility of multistate matrix we can add further layers of complexity to basic matrices in order to accommodate study systems with greater structural or modelling particularities. In the particular case of our study, we easily adapted the matrices to the particularities of the study species, with trap-dependence in breeding birds, and recovery probabilities. Further specificities of study populations may be added, such as disease status [1,2], body condition [3], and tag loss [4], among others.

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Appendix S4: Workflow, details, and analyses of our prior dispersal parameter choices

In this appendix, we discuss the prior choice for our dispersal distributions. First, we discuss our prior selection workflow. Second, we present our prior choices and discuss their adequacy above other alternative choices using data published in other studies and prior predictive checks. Third, we test the sensitivity of our models' posterior inference to prior choice.

The choice of prior distributions is an important step in Bayesian statistics and modelling [1,2,3]. In this study, we are comparing the results of models that rely on different dispersal kernel distributions. See the structure of our dispersal parameters in lognormal and gamma models:

$$Distance_{i,sex} \sim Lognormal(mean_{sex}, sd_{sex});$$
$$Distance_{i,sex} \sim Gamma(shape_{sex}, rate_{sex});$$

The prior distributions of the mean and standard deviation in the lognormal distribution and shape and rate in the gamma distribution will determine the shape of the prior dispersal kernels. Recall that in our study both distributions are truncated at a maximum value of 1200 km. A fundamental step is to find prior distributions that provide similar dispersal distance expectations for both models. This way, we can ensure priors do not affect the estimates of our models based on different distributions in significantly different ways. The information provided by prior beliefs in a model can be easily evaluated using prior predictive checks (PPC; [2,3]). PPCs are based on simulating and visualizing data from prior distributions. Using PPCs, our aim was to choose weakly informative priors that 1) encompass the range of potential values of each parameter, 2) generate reasonable values of natal dispersal distances, that is, those that encompass the range of observed distances for the Bonelli's eagle in continental western Europe in published studies [4], and 3) regularize against dispersal distance values that are considered infrequent or have never been reported according to the literature [2,4,5].

Following this workflow, by educated trial-and-error following PPCs of a range of candidate values [3], we selected normally distributed priors for both lognormal and gamma parameters, all truncated at 0 since none of both distributions accept negative values.

$$mean_{sex} \sim Normal(\text{mean} = 2.3\,, \text{sd} = 1.5);\ sd_{sex} \sim Normal(\text{mean} = 0.6\,, \text{sd} = 0.7)$$

$$shape_{sex} \sim Normal(\text{mean} = 1.2, \text{sd} = 1.2);\ rate_{sex} \sim Normal(\text{mean} = 0.04, \text{sd} = 0.05)$$

The selected prior distributions result in almost identical prior natal dispersal kernels for both distributions (Figure S12). The standard deviations of our distribution parameters appear way larger than those of any potential posterior estimate with the amount of data available. In addition, the priors encompass the range of distances published in this and neighbouring populations and regularize against extremely large natal dispersal distances that have rarely been reported ([4]; Figure S13).

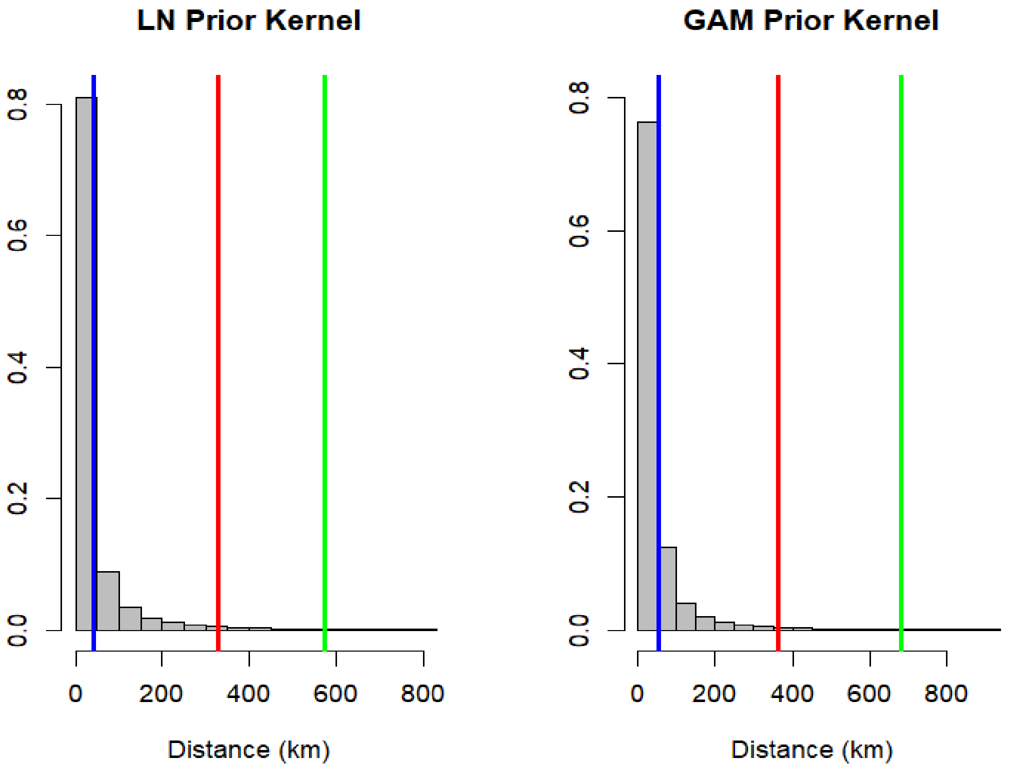


Figure S12. Mean (blue), quantile 97.5%, and quantile 99% values of lognormal (LN) and gamma (GAM) prior dispersal kernels using the selected priors.

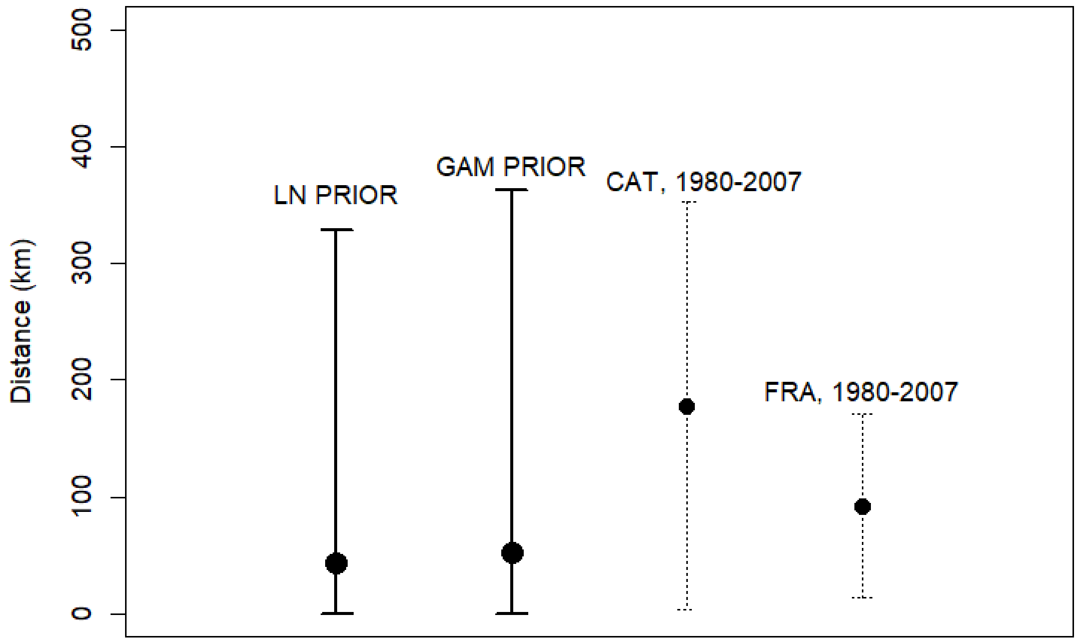


Figure S13. Mean and quantile 2.5% and 97.5% values of lognormal (LN) and gamma (GAM) prior dispersal kernels compared to the mean and equal quantiles of natal dispersal distances published for the study population, Catalonia (CAT) and the neighbouring population in France (FRA), Hernández-Matías et al. [4].

When compared to the published data in the study population and the neighbouring French population, the means of our prior dispersal kernels for both distributions are lower (Figure S13). This is because 1) dispersal distances on published articles were analysed using normal distributions, which have markedly different shapes to gamma and lognormal distributions, and 2) while published data do not account for sex, we will be splitting our dispersal estimations into sexes, and males presumably have shorter dispersal distances than females, thus we prefer to be conservative.

Although flat uniform priors may intuitively seem an adequate non-informative choice, in this situation they may even be strongly informative. Using PPCs, if we considered uniform prior distributions for both gamma and lognormal parameters that encompassed a range across and beyond the likely values of all parameters, say,

$$mean_{sex} \sim Uniform(\min = 0\,, \max = 10);\, sd_{sex} \sim Uniform(\min = 0\,, \max = 10)$$

$$shape_{sex} \sim Uniform(\min = 0, \max = 10);\ rate_{sex} \sim Uniform(\min = 0, \max = 10)$$

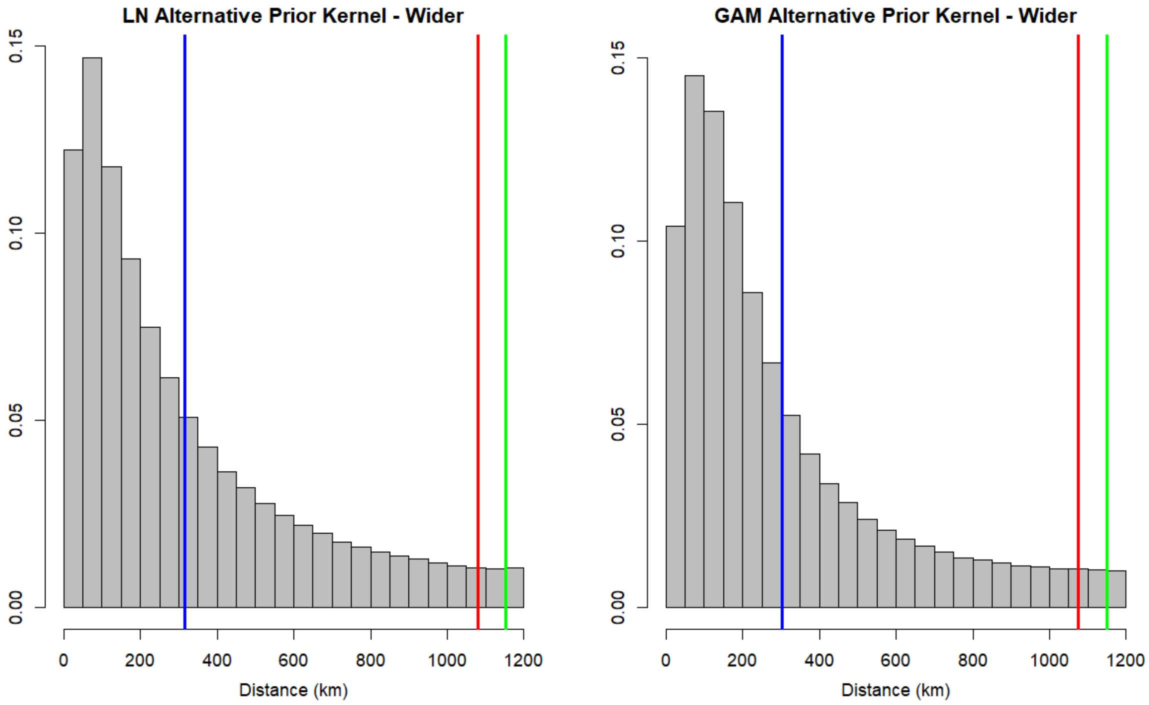
if we draw values from these prior distributions, considerable differences among distributions are generated: lognormal and gamma dispersal kernels had mean values of

4 vs 177 km, and 97.5% quantiles of 20 vs 1095 km respectively. Thus, the selected normally distributed priors are more robust choices in these cases.

One further possibility may be to use priors that reflect wider uncertainties about the dispersal kernels of both distributions between the range of distances considered in our study (i.e., 0-1200 km). Although this may also be an interesting choice, prior dispersal kernel distributions would then keep considerable prior probability densities at large and unlikely distances, which may not contribute to regularizing towards more likely values and thus not be as optimal as the priors selected in this study. However, an interesting exercise to understand the effect of our prior selection would be to analyse the sensitivity of prior choice on posterior inference (i.e., narrower weakly regularizing prior as the one chosen in our study and shown in Figure S12 vs. wider prior shown in Figure S14). We selected such wider priors by trial and error and using PPCs. We used normally-distributed priors truncated at 0 for each distribution, again focusing on obtaining similar prior distance expectations (lognormal and gamma respectively).

$$mean_{sex} \sim Normal(mean = 5.4, \mathrm{sd} = 1); sd_{sex} \sim Normal(\mathrm{mean} = 0.75\,, \mathrm{sd} = 0.3)$$

$$shape_{sex} \sim Normal(\mathrm{mean} = 2.9, \mathrm{sd} = 1);\ rate_{sex} \sim Normal(\mathrm{mean} = 0.01, \mathrm{sd} = 0.0115)$$



LN Alternative Prior Kernel - Wider

GAM Alternative Prior Kernel - Wider

Figure S14. Mean (blue), quantile 97.5%, and quantile 99% values of lognormal (LN) and gamma (GAM) prior dispersal kernels using alternative wider priors.

These alternative dispersal kernels show median distances of 212 and 202 km, 2.5% quantile distances of 17 and 16 km, and 97.5% quantile distances of 1080 and 1076 km for the lognormal and the gamma distribution respectively – that is, both kernel distributions are very similar, and show way larger expectations than the ones selected in this study (Figure S14). We compared posterior estimates of our models when using both sets of priors [1]. We did so for SEP-CAT and JOINT-CAT models (we excluded JOINT-ALL models because of their longer computation times). We compared the survival and average dispersal distance estimates obtained using both priors in the range of different models considered in this sensitivity analysis. We define the prior selected in our study as "Narrower" and the alternative prior described above as "Wider".

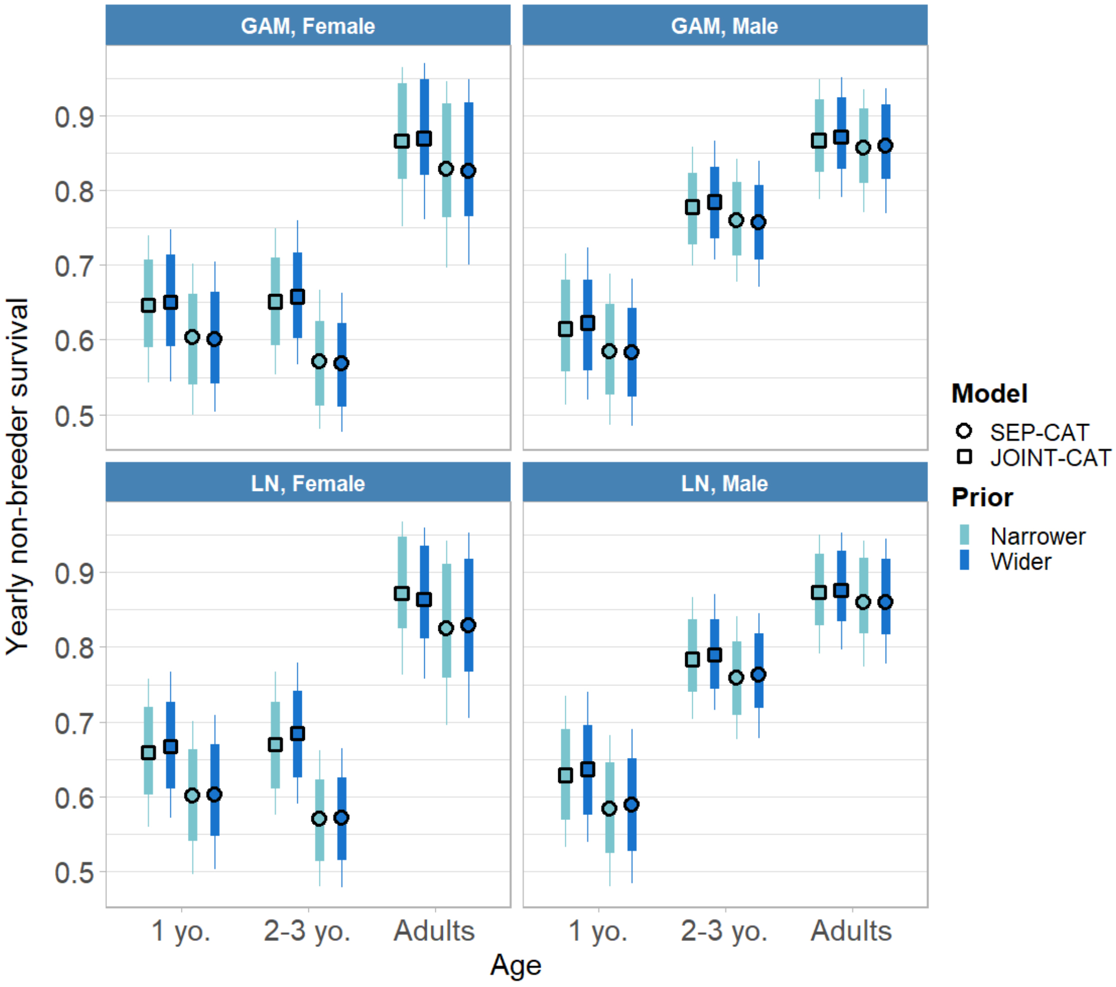


Figure S15. Non-breeder survival posterior estimates of SEP-CAT and JOINT-CAT models when using narrower priors (i.e., the ones selected in this study) with alternative wider priors. Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

The sensitivity analysis reveals very mild differences in the posterior estimates of survival (Figure S15) and average dispersal distance (Figure S16) when using the narrower priors selected in this study and alternative wider priors. Estimates of both survival and dispersal generally show very limited increases – if any - when using wider prior dispersal kernels with larger expectancies at large distances. Such slight increases appear to occur in both distributions. This suggests that 1) the effect of our selected priors on posterior inference is limited, and 2) the differences found between models and distributions are not explained by our prior dispersal kernel choices.

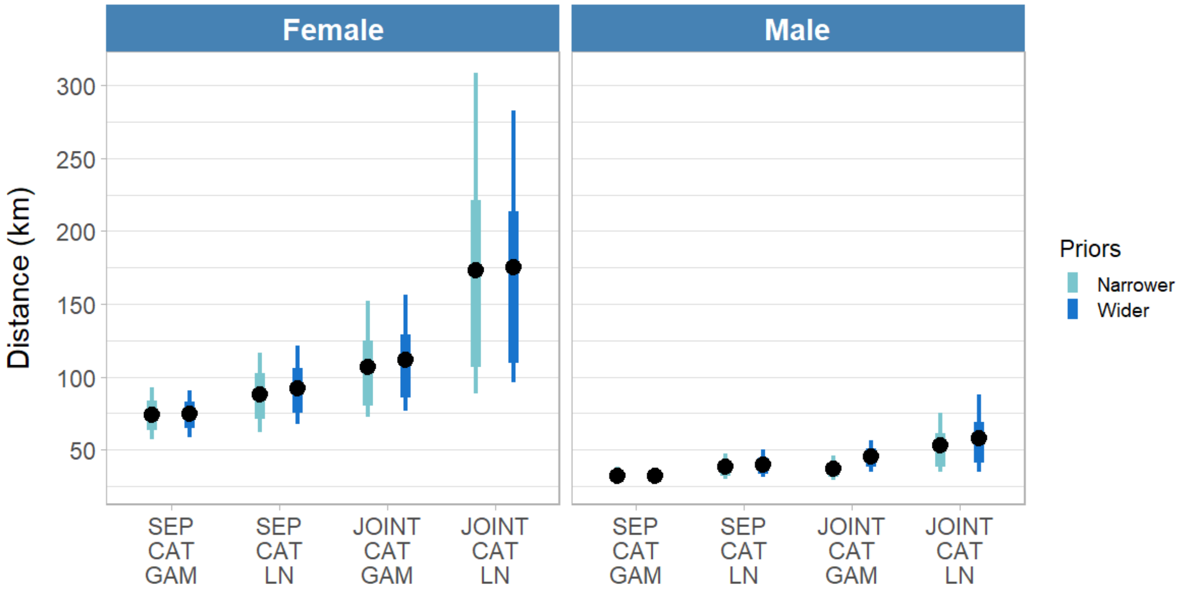


Figure S16. Posterior estimates of average dispersal distance (km) of SEP-CAT and JOINT-CAT models when using narrower priors (i.e., the ones selected in this study) with alternative wider priors. Circles and squares indicate median values. Thick lines indicate the 66% HPDI and fine lines show the 89% HPDI.

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CHAPTER 3

Fall and rise of a long-lived bird population: disentangling long-term population dynamics, sink-source status, and age-stage composition using spatially explicit integrated population models

Photograph courtesy of Jaume Elies

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Fall and rise of a long-lived bird population: disentangling long-term population dynamics, sink-source status, and age-stage composition using spatially explicit integrated population models

Author 1: Jaume A. Badia-Boher[1*]

Author 2: Antonio Hernández-Matías[1]

Author 3: Francesc Parés[1]

Author 4: Joan Real[1]

[1]Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia I Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Spain.

*jabadia@ub.edu

Abstract

Population dynamics are governed by the so-called four BIDE processes: birth, immigration, death, and emigration. However, most population models fail at explicitly considering all four processes, which may hinder a comprehensive understanding of how and why populations change over time. In this study, we employed a spatially-explicit integrated population model to thoroughly examine the long-term dynamics of a long-lived threatened raptor, the Bonelli's eagle in Catalonia (NE Iberian Peninsula) between 1986 and 2020. Our study encompassed the separate modelling of all four BIDE processes, allowing us to evaluate fine-scale long-term variations in the sink-source status, floater and breeder population sizes, and key vital rates. In addition, according to census data, the population underwent a considerable decline followed by an increase in more recent years. This fact also presented an opportunity to characterize such long-term variations during different stages of population growth. Our results showed that changes in population trends along time were determined by relatively small differences between both processes (i.e., 5-10 individuals on average). As the total and breeding population declined, the floater population was estimated as completely depleted, immigration surpassed emigration, and the population mainly functioned as a sink. In addition, immigration likely played a crucial role in mitigating declines in the breeding population. Conversely, the more recent population increases (2010-2020) were accompanied by significant improvements in non-breeder survival, substantial increments in floater population size, and increased numbers of emigrants. Additionally, the population transitioned to operating as a source in most years. Our study underscores the utility of spatially explicit integrated population models for providing a more complete understanding of population dynamics in long-lived species, allowing a joint modelling of all processes that shape population dynamics along with critical but often ignored aspects for conservation, such as sink-source dynamics and floater population sizes.

Introduction

The study of population dynamics is a central topic in population ecology and conservation. From a basic perspective, population dynamics are composed of four processes (i.e., the BIDE processes): Birth and Immigration, which provide gains to a population, and Death and Emigration, which lead to losses (Schaub & Kéry, 2021). Any changes in a population's size and trends along time is a result of changes in any of these four processes. Historically, the quantification of birth and death processes has received a larger focus (Morris & Doak, 2002). Births have often been estimated via the monitoring of breeding individuals and the number of raised offspring (i.e., fecundity or productivity; Etterson et al., 2011), and mortality has been quantified with the estimation of survival probabilities, mainly by capture-mark-recapture analyses (CMR; Lebreton et al., 1992). Instead, emigration and immigration processes are frequently ignored in population models, mainly because their estimation has traditionally been more complex. For example, estimating emigration with capture-recapture data often required additional observations from outside the study area or between sampling periods, which were frequently not available (Lindberg et al., 2001; Kendall et al., 2013). Otherwise, emigration can be implicitly accounted using apparent survival, as this type of estimate is the product of true survival and site fidelity (Lebreton et al., 1992). However, in this case both processes cannot be separately distinguished. Estimations of immigration are even more challenging methodologically, mainly because it is often impossible to differentiate immigrants from locally born individuals in a population. Because of this, population models rarely model all four BIDE processes explicitly (but see Paquet et al., 2020; Pfeiffer & Schaub, 2023). Importantly, this issue may prevent a complete understanding of population dynamics for several reasons. First, because both emigration and immigration can be key drivers of population dynamics. For instance, large emigration may lead to the decline and even local extinction of otherwise sustainable populations (e.g., Le Gouar et al., 2008; Weegman et al., 2022), and immigration may lead to the persistence of populations with large local mortalities (e.g., Schaub et al., 2010). Second, because partially or completely ignoring migration movements may prevent an understanding of the overall contribution of migration processes against local births and deaths to population dynamics and viability and their variations along time (Gilroy & Edwards, 2017; Heinrichs et al., 2019a). Third, because an explicit estimation of all four BIDE processes is essential for reliable assessments of sink-source status and dynamics, which are fundamental parameters for the demographic understanding and the effective management of spatially-structured populations (Runge et al., 2006; Hernández-Matías et al., 2013; Heinrichs et al., 2019b). Even so, sink-source evaluations are hardly ever performed considering all BIDE processes (Furrer & Passinelli, 2016; Heinrichs et al., 2019b).

Long-lived species and populations are common targets of population dynamics assessments and conservation action (Cardoso et al., 2011; Hermoso et al., 2017). These species are characterized by slow life cycles with long life expectancies, delayed maturities, and low breeding productivities (Saether & Bakke, 2000). Because of this, these populations show limited recovery capacities after disturbances, which make them especially vulnerable to anthropogenic impacts (Webb et al., 2002, Keevil et al., 2018). Importantly, long-lived species show complex dynamics that arise from their complex behavioural patterns (e.g., foraging strategies, movement patterns, territoriality), which may change along age or across both sexes, local populations, or breeding status (McNamara & Houston, 1996; Sergio et al., 2014). Such behavioural variations may lead to differences in risk exposure and mortality rates, emigration, immigration, fecundity, and first breeding probabilities among population stages (Saether & Bakke, 2000; Badia-Boher et al., 2023). Hence, the study of the dynamics of long-lived populations requires a deep understanding of their multiple population stages and the interactions between them. Nevertheless, specific population stages have traditionally received considerably lower attention, especially due to the methodological challenges in their study. For instance, monitoring schemes and research have historically focused on breeders, while non-breeding individuals often remain overlooked in demographic studies and population models (Katzner et al., 2011; Penteriani et al., 2011). Non-breeders, also known as floaters, are generally defined as those sexually mature individuals that do not breed, usually because of constraints in space or resource availability (Hunt 1998; Penteriani et al., 2011). The explicit modelling of this population stage in demographic models is essential for an unbiased estimation of key population parameters, such as survival and population growth rates (Lee et al., 2017; Plard et al., 2021). Furthermore, floaters have a central role in population dynamics with especially important implications for population stability (Penteriani et al., 2011; Katzenberger et al., 2021; Oppel et al., 2022). For example, they can be active participators in intraspecific competition processes with breeders for food and nesting resources (Bretagnolle et al., 2008). On the other hand, they often function as a pool of individuals ready to enter the breeding population when breeders die. This mechanism is known as the buffer effect and in many cases is key to sustaining stable breeding populations (Penteriani et al., 2011; Katenberger et al., 2021). In cases of high breeder mortality, the buffer effect may contribute to keeping breeding numbers constant at the expense of a continuous drainage of the non-breeding population. However, if floater populations become drained, breeder populations may decline rapidly (Penteriani et al., 2008). Besides, floaters may also be a ready source of recruits able to expand the population into new areas or territories (Hunt, 1998). Because of this, modelling the size and dynamics of floater populations along with other population stages is fundamental to assess the stability, resilience, and expansion capacity of populations.

Long-term demographic assessments may provide fundamental information on the dynamics of long-lived populations with direct management implications. Given the slow life histories of these species, long-term data may reveal demographic patterns that could remain undetected when focusing on shorter periods of time. For instance, long-term studies may provide an opportunity to understand the magnitude of fluctuations in different population stages and BIDE processes along with key demographic parameters, and the potential interactions between them in different phases of population growth. Long-term data may also reveal the magnitude of long-term variations in floater populations, of which evidence from natural populations remains scarce (Margalida et al., 2020; Oppel et al., 2022), as well as their relation with demographic rates, such as non-breeder survival, recruitment probabilities, and productivity (Ferrer et al., 2004; Bretagnolle et al., 2008; Votier et al., 2008). Besides, long-term oscillations in dispersal patterns may also be a result of changes in local or neighbouring populations, which may result into increases or decreases in the numbers of emigrants or immigrants along time (Forero et al., 2002; De Bona et al., 2019). These fluctuations, along with changes in the magnitude of birth and mortality processes resulting from changes in fecundity and survival, should be expected to lead to variations in the sink-source strength of local populations. However, little is known about how and why sink-source status may vary along time, and the potential magnitude of such variations (Heinrichs et al., 2019a). Overall, theoretical and simulation works suggest that sink or source strength may vary along time due changes in abundance, movement patterns, or habitat quality, but the long-term status of a population as a sink or a source may be strongly determined by the location of a local population in respect to the global population (Guo et al., 2005; Heinrichs et al., 2016, 2019a). The knowledge gap in the study of temporal variation in sink-source dynamics is the result of the existing methodological challenges for its estimation, which have resulted in very few published assessments, especially in long-lived species (Loreau et al., 2013; Furrer & Pasinelli, 2016; Heinrichs et al., 2016; Pfeiffer & Schaub, 2023).

The development of Integrated Population Models (IPM) is increasing our ability to model and understand population dynamics (Schaub & Abadi, 2011). This approach can combine different ecological datasets from the individual and the population level to estimate demographic parameters with increased precision. This particularity of IPMs is highly beneficial for the study of long-lived species dynamics, as often the data from different population sectors comes from different types of monitoring: information from breeding populations may arise from territory or nest watching (i.e., productivity, census, breeder survival), while survival, non-breeder and dispersal data often comes from tagging schemes. In addition, IPMs permit the estimation of demographic parameters even when there is no explicit data about them, making use of the indirect information provided by other sources of data (Schaub & Kéry, 2021). This valuable property of IPMs is particularly used to estimate immigration (Abadi et al., 2010; Schaub & Fletcher, 2015; Riecke et al., 2019; Plard et al., 2021). The development of IPMs has occurred in parallel to that of Bayesian spatially-explicit capture-mark-recapture methods (SECR; Schaub & Royle, 2014; Terui, 2020; Badia-Boher et al., 2023). These models enable the joint estimation of true survival probabilities and dispersal processes, which permits the quantification of permanent emigration along with other demographic parameters of interest. The combination of IPMs and SECR into a single modelling framework (i.e., spatially explicit Integrated Population Models, SEIPM; Chandler & Clark, 2014; Paquet et al., 2020) may provide a powerful approach to increase our knowledge of long-lived population dynamics by means of 1) estimating stage-specific vital rates and modelling the population sizes of different stages along time and their interactions, and 2) allowing the explicit modelling of emigration and immigration along with birth and mortality processes, that is, a complete modelling of the four BIDE processes.

Here, we demonstrate the usefulness of SEIPMs at disentangling the long-term dynamics of long-lived populations at a fine scale by implementing them to long-term data from a threatened raptor population: the Bonelli's eagle in Catalonia (NE Iberian Peninsula). This population was intensively monitored between 1986 and 2020 using mark-reencounter schemes, breeding territory counts, fecundity surveys, and information about individual replacements in breeding nests. In addition, according to census data, the population encompassed a phase of decline (1986-1999), stability (2000-2007), and subsequent increase in population size (2008-2020). In this scenario, we aimed at 1) explicitly modelling all four BIDE processes and understanding their contribution to the overall dynamics of the population, population growth rates, and sink-source dynamics, and 2) understanding long-term variations in different population stages (i.e., breeders, floaters, recruits) and key demographic parameters (i.e., sink-source status, survival, recruitment rates, productivity) under different phases of population growth. To perform these estimations, we integrated all mentioned demographic datasets into an SEIPM. To estimate true non-breeder survival and emigration, we used the multistate SECR framework developed by Badia-Boher et al. (2023). In addition, to estimate breeder survival, we used an extension of the method provided at Hernández-Matías et al. (2011a) specific for territorial populations. Finally, we evaluated the elasticity and sensitivity of key vital rates using perturbation analyses (Caswell, 2000; Schaub & Kéry, 2021) We expect our results to define a useful framework to develop powerful spatially explicit Integrated Population Models to disentangle the dynamics of long-lived populations at finer scales. Additionally, we aim at providing a deeper understanding about long-term variations in key demographic parameters and population stages in long-lived species.

Methods

Study species and data collection

The Bonelli's eagle is a long-lived territorial raptor with delayed maturity and low breeding rates whose range extends from south-east Asia to the western Mediterranean. It is assessed globally as Least Concern, but as Near Threatened in Europe and Endangered in Spain, where the species suffered considerable declines and local extinctions in the late 20th century (Birdlife International, 2015, 2019). As in many territorial species, Bonelli's eagles show a non-territorial nomadic behaviour after the post-fledging dependence period, with regular visits to areas with high prey densities away from breeding territories (Real & Mañosa, 2001). After sexual maturity, individuals tend to establish into territories and recruit to the breeding population. Although this happens at a variable age, individuals often recruit between three and four years of age (Hernández-Matías et al., 2010). At this point, birds start displaying territorial and pair-binding behaviour, and show very strong fidelity to their first partners and first breeding areas throughout their lives (Hernández-Matías et al., 2011b). Thus, in this article we referred to breeders as individuals that held a territory, and non-breeders and floaters to non-territorial individuals. Besides, breeding dispersal is very rare in this species and may only involve very short distances. Because of this, recruitment to a first breeding territory outside a local population practically always results into permanent emigration (see Badia-Boher et al., 2023). Individual ages are easily characterized because of plumage patterns, which allow the differentiation of juveniles (1 year old), immatures (2 years old), subadults (3 years old), first-year adults (4 years old), and adults (5 years old and older).

Our focal population is located in Catalonia (NE Spain), where the species suffered a sustained decline from ca. 82 breeding pairs in 1986, to an observed minimum of ca. 64 pairs in 2000, followed by a phase of stabilization in numbers (2000 – 2007) and a recent recovery to reach ca. 81 pairs in 2020. We used data collected between 1986 and 2020. Data from the breeding population was obtained from the monitoring of territories between January and May every year (i.e., the breeding season), and included several visits per breeding season to 1) determine the occupancy status of territories (abandoned or occupied), 2) detect changes in the composition of breeding pairs, and 3) record reproductive parameters (i.e., productivity). In addition, two different intensive ringing and resighting schemes were launched (1986-1999 and 2008-2020) where eagles were ringed as chicks in their nests with both metal and alphanumeric colour rings. In total, 596 chicks from 51 different territories were ringed. Resighting efforts were concentrated on breeding territories and dispersal areas of non-breeders, which resulted in 196 eagles being recontacted alive, of which 95 detected as breeders. In addition, 103 eagles were recovered dead from the surveillance of territories, dispersal areas, and zones of high mortality risk (i.e., power infrastructure, ponds) by monitoring and ranger teams.

Integrated Population Model

We combined capture-mark-recapture (CMR), productivity, count, and territory replacement data into a Bayesian Integrated Population Model (IPM) to estimate population size and demographic parameters along time in a single analytical framework with improved precision (Schaub & Abadi, 2011). Territory replacement data were modelled in a multievent CMR framework to estimate survival of breeders (Hernández-Matías, 2011a, 2013). Productivity and count data provided information on breeder fecundity and breeder population size respectively. All these parameters were estimated as time varying. CMR data were modelled to estimate true survival, permanent emigration probabilities, and recruitment to the breeding population using a spatially-explicit framework (Badia-Boher et al., 2023). Because the relatively limited amount of data available did not allow the modelling of temporal variation, we modelled them as fixed for three different phases corresponding to the available CMR datasets, which match reasonably well the phases of population growth observed from census data: declining (1986-1999), stable (2000-2007), and increasing (2008-2020).

The essential step in an IPM formulation is to adequately link all estimated demographic parameters from the different ecological datasets considered to a state-space model of population dynamics that reflects the life cycle of the study species (Figure 1).

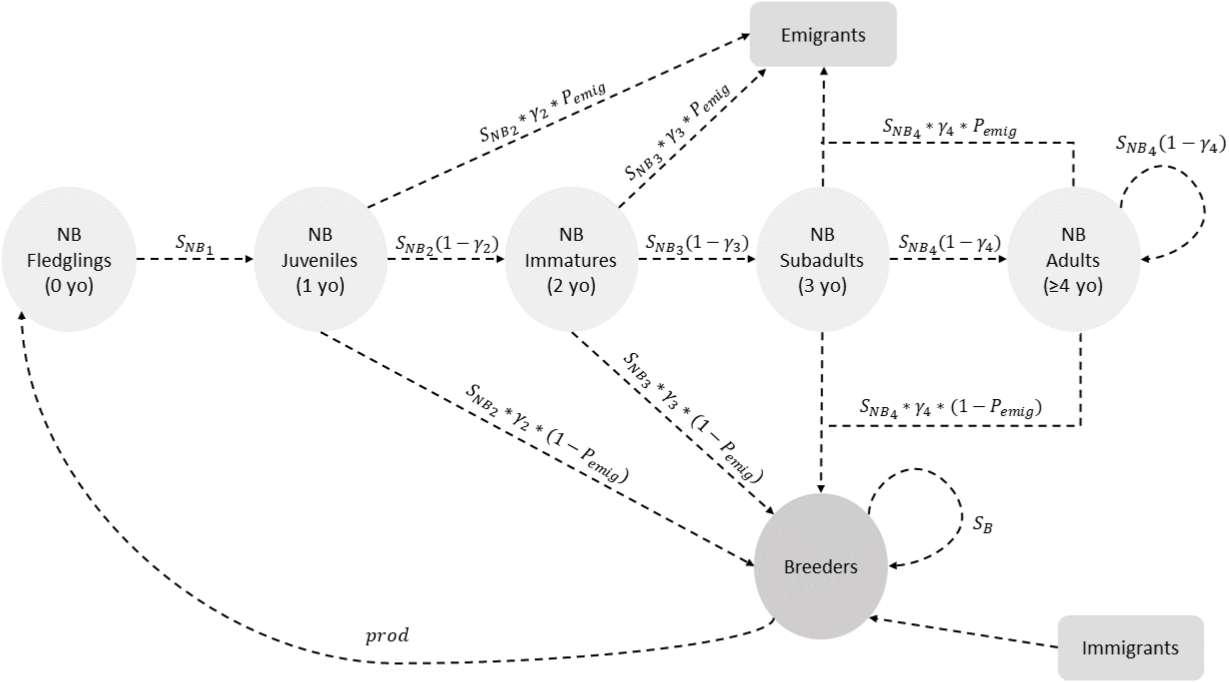

Figure 1. Life cycle of the Bonelli's eagle population as modelled in the state-space population dynamics model. Text circles and squares indicate different population stages. Dashed arrows indicate transitions between population stages. Abbreviations NB, B, and yo stands for "Non-Breeder", "Breeder", and "years old" respectively. Parameters S, Y, prod, and P_{emig} stand for "Survival", "Recruitment to the breeding population", "Productivity", and "Permanent emigration" probabilities respectively. Subindices 1 to 4 indicate ages juvenile (1yo.), immature (2yo.), subadult (3yo.), and adult (4yo. and older) respectively.

Based on a post-breeding census, and considering demographic stochasticity based on a Poisson distribution, we modelled birth of individuals as:

$$N_{fledglings_{t+1}} \sim Poisson(N_{B_t} * S_{B_t} * prod[t]),$$

where *prod*, *t*, S_B, and N_B stand for productivity, time (year), breeder survival, and breeder population respectively. Fledglings may survive to later ages and remain as non-breeders:

$$N_{NB_{age+1,t+1}} \sim Poisson\left(N_{NB_{age,t}} * (1-\gamma_{age,t}) * S_{NB_{age,t}}\right),$$

where N_{NB} and γ stand for non-breeder population size and recruitment to the breeding population respectively. Instead, individuals may recruit and hence join the breeding population. Since natal dispersal, and subsequently, permanent emigration and permanent immigration occur at the time of recruitment to the breeding population, we accounted for these parameters at this stage (Badia-Boher et al., 2023). Hence, according to permanent emigration probability P_{emig}, individuals may recruit inside the local population ($1-P_{emig}$) or outside of it (P_{emig}). The total number of breeders at year *t* must also include the number of permanent immigrants (N_{imm}).

$$N_{B_{t+1}} \sim Poisson\left(\left(N_{B_t} * S_{B_t}\right) + \left(N_{NB_{age,t}} * S_{NB_{age,t}} * \gamma_{age,t} * \left(1 - P_{emig_t}\right)\right) + N_{imm_t} \right),$$

The number of permanent emigrants is thus calculated as follows:

$$N_{emig_{t+1}} \sim Poisson\left(N_{NB_{age,t}} * S_{NB\,age,t} * \gamma_{age,t} * P_{emig_t}\right)$$

Note that because of their definitions, both yearly emigrant and immigrant numbers (N_{emig} and N_{imm}) are equivalent to the numbers of yearly emigrant and immigrant recruits. In addition, the number of yearly recruits born in the study population (i.e., local recruits, N_{lr}) can be easily retrieved:

$$N_{lr_{t+1}} \sim Poisson\left(N_{NB_{age,t}} * S_{NB_t} * \gamma_{age,t} * \left(1 - P_{emig_t}\right)\right)$$

Immigration was the only process for which no direct data were available. Thus, as is commonplace in IPMs, we estimated immigrant population size as a hidden parameter, taking advantage of the indirect information provided by the datasets included in the study (Abadi et al., 2011). This indirect information is contained in the difference between the observed breeders counts and the expected population trajectory under the demographic rates estimated in the IPM. Following Schaub & Fletcher (2015), we estimated immigration as an absolute number: $N_{imm_t} \sim Poisson(\Omega)$. Because we did not have enough precision to estimate Ω yearly, we assumed that Ω was constant for each period of growth in the study population (i.e., decreasing, 1986-1999; stable, 2000-2007; increasing, 2008-2020). For each period, our prior belief was that the number of immigrants would follow a uniform distribution between 0 and 30 individuals: $\Omega_t \sim Uniform(0,30)$.

Productivity data

To estimate productivity (i.e., the number of chicks fledged per breeding individual), we monitored the yearly number of fledglings raised (J) from monitored breeding pairs (M; 46 on average, 20 min, 73 max). We assumed that productivity followed a gamma distribution with prior $prod_t \sim Gamma(1{,}1)$. We modelled the number of fledglings following a Poisson distribution that was the product of productivity (*prod*) and the number of monitored pairs: $J_t \sim Poisson(M_t * prod_t)$, and divided it by two to obtain productivity values per individual (Kéry & Schaub, 2012).

Floater population calculations

The floater population was defined as the sum of non-breeders aged 3 or older. We assumed this age class composition because of the available knowledge about the species, as individuals hardly ever recruit and/or compete for breeding territories when they are juveniles, and most immatures (i.e., 2-year-olds) still do not show territorial behaviours (Hernández-Matías et al., 2010; Badia-Boher et al., 2023). Instead, most subadults (3-year-olds) and older eagles already show territorial patterns, thus generally contributing to the buffer effect and intraspecific competition (Penteriani et al., 2011).

Breeder count data

We modelled the number of breeding individuals per year using data on yearly breeder population counts. The yearly observed numbers of breeders C_t were the response variable of a Normal distribution $C_t \sim Normal(N_{B_t}, T_t)$ where N_B is the number of breeding (territorial) individuals estimated in the IPM's population dynamics model and T_t is a precision parameter to accommodate uncertainty in the estimate resulting from observation error and the model's lack of fit (Schaub & Kéry, 2021).

Sink-source calculation

To estimate the sink-source status of the local population in Catalonia in respect to the global Bonelli's eagle spatially-structured population in western Europe, we calculated the population-specific per capita contribution metric, C^r, proposed by Runge et al. (2006). This metric includes population growth, emigration, and immigration in the calculation of a population's contribution to the global metapopulation, while considering emigration as a positive contribution, and immigration as a negative contribution. We followed the formula $C_t^r = \lambda_t + E_t - I_t$, where λ stands for the local population's growth rate, and E and I stand for the population's numbers of emigrants and immigrants in respect to the total size of the local population.

Sensitivity and elasticity analyses

We used perturbation analysis to identify the vital rates that had the strongest effects on population dynamics considering breeder survival, non-breeder survival, and productivity (Caswell, 2000; Morris & Doak, 2002). Namely, we calculated the absolute (i.e., sensitivity), and the relative increment in the population growth rate in relation to an increment in the target vital rate (i.e., elasticity). We used the matrix population model and all vital rates estimated in our SEIPM for our calculations.

Non-breeder survival, recruitment, and permanent emigration estimation

We modelled life-encounter and natal dispersal data jointly using the spatially-explicit capture-mark-recapture model (SECR) described at Badia-Boher et al. (2023). This formulation addresses the interdependence between resighting and dispersal probabilities to estimate an individual's probability to recruit into a breeding territory outside a local study area (i.e., permanent emigration) along with true survival probabilities. The model is based on two submodels: a CMR submodel for life-encounter data and a spatial submodel for natal dispersal data.

The modelling of life-encounter data was based on a hierarchical state-space design in a multistate CMR formulation with two components. First, the state process described by the state-transition matrix *ps*, which defines how individuals *i* change their biological states *z* between consecutive occasions *t* following a categorical distribution (Kéry & Schaub, 2012):

$$z_{(i,t+1)} | z_{i,t} \sim Categorical(ps_{z_{i},t}, i, t, 1{:}S)$$

where S is the number of states considered. Second, the observation process described by the observation matrix *po*, which indicates how individual observations *y* relate to the states of the individuals.

$$y_{i,t} | z_{i,t} \sim Categorical(po_{z_{i,t}}, i, t, 1{:}O)$$

where O is the number of observations considered.

The natal dispersal submodel modelled 1) natal dispersal distances, and 2) subsequent recruitment to a breeding territory either inside or outside the study area, conditional on the modelled dispersal distance. To model natal dispersal distances, we assumed isotropic conditions (i.e., dispersal direction was uniform across the range of the species; Dupont et al., 2022). For individuals observed as breeders, natal dispersal distance was calculated as the distance between the territories of birth and recruitment. For the rest, distances were modelled as random draws from a lognormal distribution, based on its generally better adequacy to model natal dispersal in this species (Badia-Boher et al., 2023; Fandos et al., 2023). To model recruitment to a breeding territory, we considered all breeding territories in the western European range of the species following a point process (i.e., 916 territories in Spain, Portugal, and France; del Moral & Molina, 2018; Badia-Boher et al., 2023). Individuals would recruit to the closest breeding territory to their drawn natal dispersal distance. If that territory happened to be outside the study area, the individual would be considered as a permanent emigrant. To link this natal dispersal model with the multistate CMR model and jointly estimate all demographic parameters, permanent emigration was modelled in the state transition matrix *ps* as a transition from a live non-breeder state to a permanently unobservable state (i.e., the Absorbing state). The whole SECR framework is described in more detail at Badia-Boher et al. (2023).

Based on this formulation, we built two different SECR models, one for each tag-resighting dataset available during the study period (i.e., 1986-1999 and 2008-2020). Both models included dead recoveries from the whole range of the species in western Europe and live observations within the same geographic range (i.e., Catalonia, France, and the administrative provinces of Valencia and Alacant). Both models provided estimates of true survival, recruitment to the breeding population, permanent emigration, resighting, and recovery probabilities. True survival was structured by age and breeding status, while recruitment was structured by age, and resighting and recovery probabilities were structured by breeding status. In addition, we set recruitment as 0 for juveniles, given the very low recruitment rates detected at that age (i.e., 0-1%, Hernández-Matías et al., 2010; Badia-Boher et al., 2023), To model natal dispersal, we used the weakly informative priors selected at Badia-Boher et al. (2023). For the rest of estimates, we chose vague priors following a beta distribution: $Estimate \sim Beta(1,1)$. To avoid violation of the instantaneous sampling assumption, we pooled sampling occasions into six-month periods: January to June, and July to December (Lebreton et al., 1992). Since breeders were only monitored during the breeding season (i.e., January to June), we set breeder resighting probabilities to 0 from July to December. The number of states, observations, and specific number of parameters of both models varied to adapt to the particularities of each dataset. In particular, 2008-2020 data contained a larger number of ringed individuals and allowed for more complex age structures in survival and recruitment. In addition, 2008-2020 data required accounting for breeder detection heterogeneity (Badia-Boher et al., 2023) and for 1986-1999 it was necessary to account for tag loss (Real & Mañosa, 1997). Since no tagging schemes were active between 2000 and 2007, we assumed estimates of true survival and recruitment probabilities from a neighbouring conspecific population with similar demographic features for the same period (see subsection "2000-2007: Stable phase" and Appendix S2). As mentioned earlier, the relatively low sample sizes of our CMR datasets - a typical issue in long-lived and threatened populations – prevented an estimation of demographic parameters as varying by year. However, because the three considered periods with estimated demographic parameters (i.e., 1986-1999, 2000-2007, 2008-2020) coincide quite well with three different phases of population growth in the study population, our estimates may already be capturing the most relevant variation in these demographic parameters along time. Here below, we detail the parameterization of each SECR model and the rationale, assumptions, and model checks of our assumptions.

1984-1999: Declining phase

We estimated non-breeder survival, recruitment, natal dispersal, and permanent emigration based on a mark-reencounter scheme launched between 1986 and 1999, which involved the tagging of n = 130 individuals as chicks of which 18 were recontacted alive, 12 were detected alive as breeders, and 28 were recovered dead. Birds were marked with both PVC alphanumeric rings and metal rings. There is evidence that loss of both PVC and metal rings was present (Real & Mañosa, 1997), and thus we accounted for it in our models following the structures of Badia-Boher et al. (2019) and assuming a constant loss rate along time. Overall, we defined 13 different states (see Appendix S1) accounting for individual live status (i.e., alive vs. dead), breeding status (non-breeder vs. breeder), the rings carried by the bird (both vs. PVC vs. metal), the recovery status at death (unrecovered vs. recovered) plus the Absorbing State (AS, also known as the Long-Dead state, a permanently unobservable state). Individuals may become permanently unobservable if they 1) lose both rings, 2) recruit to a breeding territory outside the study area (i.e., permanent emigration), or 3) die and are not recovered. Survival was modelled as varying between non-breeders and breeders, and in non-breeders, it varied between juveniles and older ages. Recruitment to the breeding population was estimated as varying between immatures and older birds. Recovery probabilities were estimated as constant. We defined 13 types of observations with similar definitions to the chosen states (See Figure S1) and estimated resighting probabilities as varying between breeders and non-breeders to accommodate known detection heterogeneity (Hernández-Matías et al., 2011b).

2000-2007: Stable phase

Because no mark-resighting schemes were available between 2000 and 2007 in the study population, we used estimates of non-breeder survival and recruitment from the contiguous French population (Hernández-Matías et al., 2011b). Both populations showed very similar dynamics along time in the last decades, which is probably a reflection of very similar environmental conditions and similar levels of mortality threats between them (Figure 2). In fact, the distribution of both populations shows a continuum along the Mediterranean coast. Because of this, resightings and recoveries of individuals between both populations are often reported and included in mark-recapture analyses. For example, the study from which estimates of the French population were assumed (i.e., Hernández-Matías et al., 2011b) included individuals born in France and recruited in Catalonia, as well as dead recoveries in the area. In addition, non-breeder survival and recruitment estimates of the French population were already assumed for the modelling of the Catalan population during the 1990-2005 period by Hernández-Matías et al. (2013) and provided a good fit to the observed population trends in the area, which adds further support for the adequacy of these estimates.

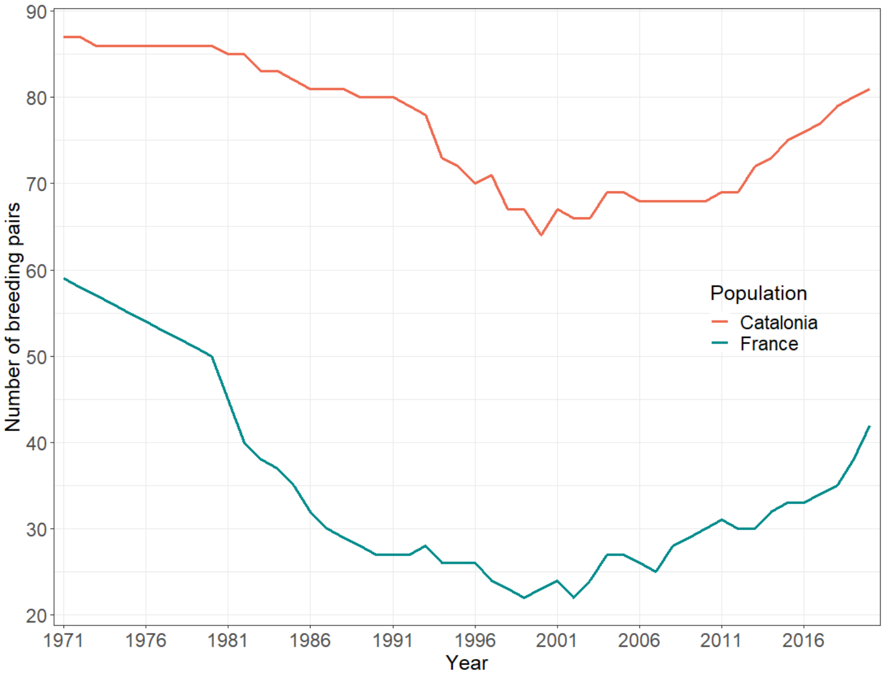

Figure 2. Dynamics of the Catalan and French breeding populations according to census data (1971-2020).

Nevertheless, in Hernández-Matías et al. (2011b), survival was estimated in a non-spatial CMR framework. Hence, we may be at risk of using estimates of apparent survival biased by permanent emigration (i.e., apparent survival) for this period while using true survival in the other two periods. Hence, to avoid any survival underestimations, we performed simulations to assess the magnitude of differences between true and apparent survival in the estimates of Hernández-Matías et al. (2011b). First, we simulated encounter histories based on the demographic parameters reported in the study. Second, we analysed these simulated data under 1) a conventional multistate CMR model, and 2) a SECR model using natal dispersal data for the same population and period provided at Hernández-Matías et al. (2010). We compared the resulting estimates of survival of both types of models, which showed no differences (<1% on average, Figure S9). Further details on the approach taken in the simulations and model results are provided at Appendix S2, Figures S6 to S9, and Table S1 therein. Such absence of differences between apparent and true survival contrast with the findings for the local population of this study (i.e., Catalonia), where differences are considerable (Badia-Boher et al., 2023). These contrasting patterns are probably explained because most individuals from the French population recruited within their population of origin, which is probably caused because of the relatively isolated geographical situation of the French population, at the northeastern limit of all western European populations (Hernández-Matías et al., 2010; Lieury et al., 2016). Additionally, the study area in France was considerably larger than that in Catalonia and the French study already incorporated resightings in the neighbouring Catalan population, thus providing an increased ability to estimate true survival (Dupont et al., 2022). In agreement with our findings, we used the estimates of (true) survival and recruitment from the French population in our study for the period 2000-2007. We incorporated the mean values and associated uncertainties as priors. However, we assumed permanent emigration probabilities calculated for the Catalan population during 2008-2020, which we considered a reasonable assumption to avoid an underestimation of emigration rates given the differences in the dimensions of the different study areas, in natal dispersal, and in permanent emigration probabilities found between both populations (Hernández-Matías et al., 2010; Appendix S2).

2008-2020: Increasing phase

To estimate demographic parameters for this phase, we used the same modelling structure as Badia-Boher et al. (2023). We used data on life-encounter and recovery data of 461 eagles ringed as chicks tagged with both metal and colour alphanumeric rings. Tag loss was prevented by riveting all rings. In total, 178 birds were resighted alive, 83 of which as breeders, and 75 were recovered dead. Here, we defined 5 states (Figure S2) accounting for survival status (alive vs. dead) and breeding status (breeder vs. non-breeder). We also defined 5 types of observations in the observation matrix equivalent to the definitions of states (Figure S3), and we accounted for breeder detection heterogeneity (breeder seen for the first time vs. seen in subsequent occasions) to accommodate variations arising from the specific field monitoring design of this period. See *Methods* at Badia-Boher et al. (2023) for further details. Non-breeder survival was structured by age (juveniles vs. immatures and subadults vs. adults) as well as recruitment (juveniles vs. immatures vs. subadults vs. adults).

Breeder survival estimation based on territory replacement data

We estimated yearly survival of breeders based on territory replacement data using turnover rate methods (TOR) adapted to the multievent CMR formulation for an improved incorporation and propagation of uncertainty (Hernández-Matías et al., 2011a). TOR methods focus on changes in the compositions of breeding pairs in territories (i.e., replacements), and the attribution of these changes to either mortality or other sources (i.e., dispersal, abandonment) for a fine estimation of survival (Hernández-Matías et al., 2011a; Oppel et al., 2021). The implementation of the method requires that 1) territory locations are conserved along time, so that they are predictable, and the study species shows strong fidelity to them, 2) replacements can be at least partially identified by changes in the features of the individuals (i.e., plumage, size, fur characteristics, or tags), and 3) the sex of each breeder must be assignable with certainty, so that the replaced individual in a pair can be known with confidence. An important advantage of this method is that it allows accounting for survival information stemming from unmarked individuals, thus enabling larger estimate precisions. The Bonelli's eagle is an ideal species to implement the TOR approach, as age until adulthood can be assessed by plumage changes. In addition, sex is easily ascertained based on behaviour (e.g., courtship, copulation, and incubation) and body size differences (del Hoyo et al., 1992). Individual replacements may be detected by observing marks using telescopes if the individual is ringed, or by changes in the plumage incompatible with aging in any of the breeders. Yet a fraction of replacements may not be observed (i.e., mainly adult-to-adult replacements), this can be accounted in the estimation of survival by the estimation of non-observable replacement probabilities (NOR). This probability is inferred based on the proportion of non-adult individuals in the breeding population, which shows a strong negative correlation with NOR probabilities (Hernández-Matías et al., 2013). A more detailed description of TOR methods is provided at Hernández-Matías et al. (2011a).

We adapted the method to the Bayesian multievent formulation because this approach facilitated a more detailed estimation of all parameters that may affect the territory replacement observation process accounting for all uncertainties present in the study system. For instance, observation effort and territory abandonment probabilities could be explicitly modelled. Additionally, NORs probabilities could be only implemented to untagged individuals and not to the whole general population as conventionally done.

Furthermore, we could address the conventional assumption that replacements are all caused by mortalities. Although infrequent, some replacements or disappearances may be due to breeding dispersal or expulsions by conspecifics (hereafter, "abandonments", n = 26 events observed between 1986-2020). The ability of multievent models to deal with uncertainty in state assignment is ideal to treat this type of uncertainty (Pradel, 2005).

We designed a multievent formulation using sex-specific spots in each territory as modelling units. We modelled changes in occupancy and replacement status of territory spots (i.e., full, empty, replacement by mortality or other causes) to estimate survival. Our model considered whether individuals in territories were marked in order to model replacements with different degrees of certainty. In the case of marked individuals, replacements were assumed to be observed with certainty (see Badia-Boher et al., 2023), while in unmarked birds a probability of a NOR between consecutive occasions was estimated. This estimation was carried out using the yearly proportion of non-adults in the breeding population as the explanatory variable and NOR probability as the response variable, following the linear equation between both variables estimated at Hernández-Matías et al. (2013). In addition, we used information on reported breeding dispersal events, conspecific expulsions, and recoveries of dead breeders to assign replacements or individual disappearances to either mortality or abandonment. Whenever the type of replacement was unknown, this was considered as an uncertain state, which was dealt with by estimating the probabilities of assigning an unknown disappearance as either a mortality (rM) or an abandonment (rA).

We built encounter-history matrices in which each row was a sex-specific spot in a territory (i.e., row 1: Territory 1 – Female; row 2: Territory 1 – Male; row 3: Territory 2 – Female; and so on), and each column was a given year (1986 – 2020). We differentiated between events (i.e., what the observer perceives about the state of a territory spot) and states (i.e., the true state of the territory spot). Events were: 1) Already empty spot, 2) Abandonment resulting in empty spot, 3) Mortality resulting in empty spot, 4) Individual disappearance of unknown reason resulting in empty spot, 5) Spot already occupied, no replacement, 6) Abandonment, replaced by new individual, 7) Mortality, replaced by new individual, 8) Individual disappearance of unknown reason, replaced by new individual, 9) Unobserved spot. On the other hand, the model states were defined as 1) Empty, 2)

Abandonment resulting in empty spot, 3) Mortality resulting in empty spot, 4) Spot occupied, no replacement, 5) Abandonment, replaced by new individual, and 6) Mortality, replaced by new individual. Note that we differentiated individual disappearances that led to empty male/female territory spots from those that led to the entrance of another individual. We did this because disappearances that resulted in empty spots could be observed with certainty, and thus modelling NORs was not necessary in those cases. Thus, in this state/event formulation, a spot in a territory may be observed as occupied by the same individual with no replacement (event 6) but be in the true state 6 (mortality) following the probability of a NOR at that specific occasion. In addition, following the requirements of multievent models, we built initial state vectors and initial event matrices, which gathered the proportions of territory spots in each state and event at first sampling occasion (Pradel, 2005; Jan et al., 2019). Initial state proportions were calculated using a Dirichlet distribution (Jan et al., 2019). The initial event matrix had the same structure as the event matrix. Because some territories started or stopped being monitored at specific years (mainly because they had been completely abandoned years before), we conditioned each row (i.e., territory spot) on first and last sampling occasion. We modelled breeder survival as a year-varying probability. Observation effort, conceived as the probability of observing the individual that belongs to a territory spot in a specific year, was also modelled as time-varying. The assignment probabilities *rA* and *rM* were modelled as constant along time. In addition, to model transitions between empty and occupied spots and territory abandonments, we estimated the probability of colonizing an empty territory spot (*c*), and the probability of fidelity of a live individual to a territory spot (*f*). Live individuals would perform territory abandonment following 1-*f* or remain in it following *f*. Both *c* and *f* were modelled as constant probabilities. A detailed representation of state transition matrices, event matrices, and parameters used was provided at Figures S4 and S5. All parameters were defined with uninformative priors bounded between 0 and 1: Parameter ~ Beta(1,1). We integrated this model in our SEIPM and used the resulting breeder survival estimates for population modelling.

Model implementation and goodness of fit

The model was run in 4 MCMC chains for 160000 iterations, of which the first 110000 were discarded. Samples were thinned by a factor of 4. We determined MCMC convergence using the Brooks-Rubin-Gelman diagnostic (Brooks & Gelman, 1998) and visual inspection of MCMC chains. All parameters presented R-hat values below 1.02 (lower than the traditional threshold set at 1.1). The general approach to evaluate the goodness of fit (GoF) of IPMs is to explore separately each different submodel (Besbeas & Morgan, 2014). For multistate CMR data, we used the GoF test for the Jolly-Movement model in software U-CARE (Choquet et al., 2009), which showed an adequate fit for both datasets (p-values = 0.981 and 0.373 for the 1986-1999 and 2008-2020 datasets respectively). For breeding count and productivity data, we performed posterior predictive checks (PPC), which are based on comparisons between observed and model-simulated data (Kéry and Schaub, 2012). The fit is evaluated using Bayesian p-values: values close to 0.5 show adequate fit to the data, while values above 0.975 and below 0.025 show a poor fit. The checks show a very adequate fit of the model to count (p-value = 0.43) and productivity data (p-value = 0.47). Results are provided using mean posterior values and 90% credible intervals (CRI).

Results

Population size along time

The estimated total population size started at avg. 311 individuals in 1986 and kept relatively stable numbers (i.e., 321 individuals, 90%CRI = 278-365, in 1989) until a progressive decrease towards a minimum of ca. 236 individuals (210-265) in 2002 and a recovery to numbers similar to those at the beginning of the study (2020: 325 individuals, 287-361). The breeding population followed a similar trend, starting from 162 individuals (160 – 164) in 1986, decreasing to a minimum of 132 (129-134) in 2001, and starting a progressive recovery especially visible in the decade of the 2010s, until the last study year (i.e., 2020, 162 individuals, 159-164; Figure 3). The floating population showed very low numbers until the early 2000s (i.e., 2-3 individuals, 0-7, at most years), but progressively increased afterwards (e.g.,12 individuals, 5-28, in 2005) to reach 26 individuals (9-42) in 2020 (Figure 3).

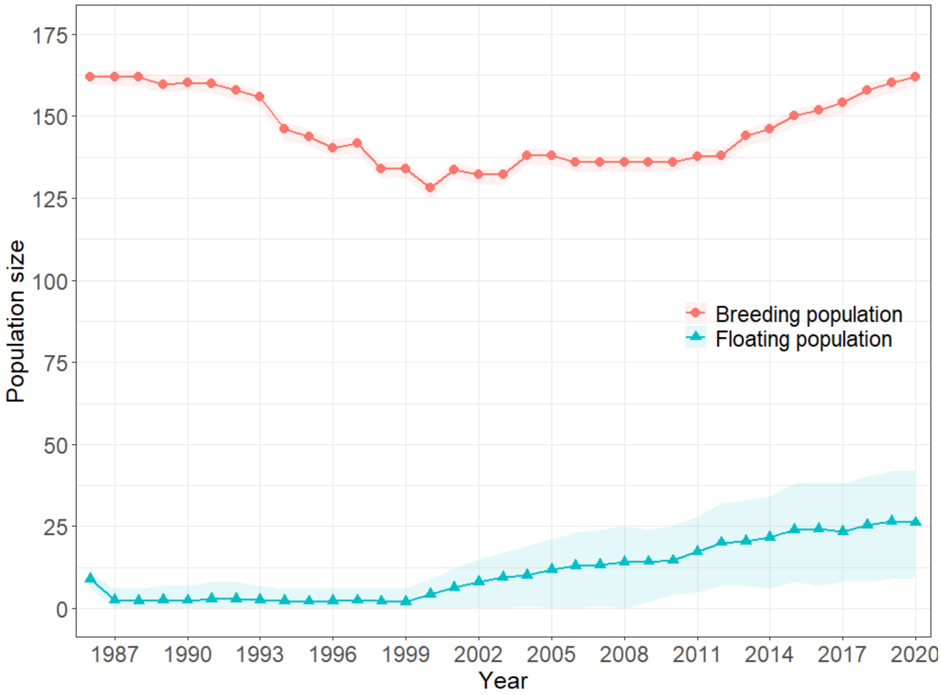

Figure 3. Yearly numbers of individuals in the floating and the breeding population (1986-2020). Points show posterior mean values and shaded areas show 90% credible intervals.

Mortality in the study population was on average larger than births coinciding with the observed population decline (1986-2004), followed by years with similar numbers (2005-2010) and a latest phase in which births exceeded mortalities (2011-2020; Figure 4). Both the numbers of births and deaths showed a general decrease throughout the course of the study. As an example, 103 fledglings (66-134) were born in 1988; and 68 fledglings (45-88) in 2020. In addition, 90-105 birds used to die (70-120) yearly between 1986 and 1990, and around 50 and 60 (40-70) in latest years. The immigrant population size showed stable values between 1986 and 2007 (8-9 individuals, 1-16), showing a mild decrease afterwards (i.e., 2008-2020, 5-6 individuals, 0-12). Average emigrant population size oscillated between 2 and 5 individuals (0 – 7/8) between 1986 and 2007, showing a sensible increase between 2008 and 2020 (6 individuals on average, 2-10).

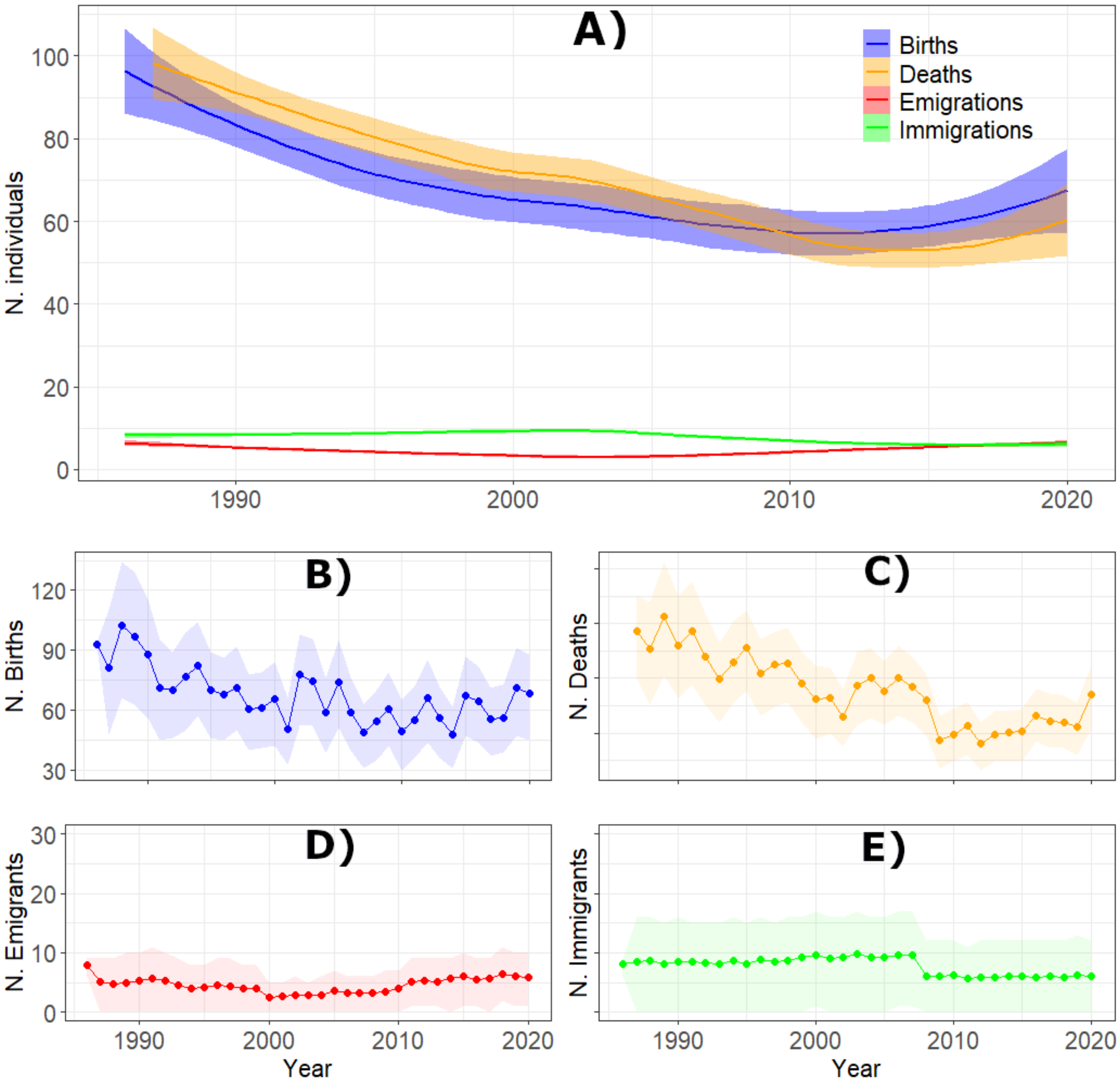

Figure 4. Numbers of births, deaths, emigrants, and immigrants in the study population (1986-2020). Subpanel A) shows smoothed population trends with local polynomial regression and associated standard errors for each demographic process. In subpanels B) to E), points show posterior mean values and shaded areas show 90% credible intervals.

The yearly number of local recruits decreased from 7 (4-10) in 1987 down to a minimum of 5 (2-7) in 2000, and progressively recovered to ca. 12 (8-16), being the major source of recruits from 2009 to 2020 (Figure 5). Immigrants were the largest source of recruits between 1986 and 2008 although with large uncertainty associated (e.g., 10, 1-17 immigrants in 2000 as a peak value). The numbers progressively decreased until being approximately half less abundant than local recruits in 2020. The number of emigrant recruits followed a similar trend than that of local recruits but was always ca. 50% lower.

Note that because of the definition of immigrants and emigrants, the numbers of recruits is equivalent to the global numbers of immigrants and emigrants.

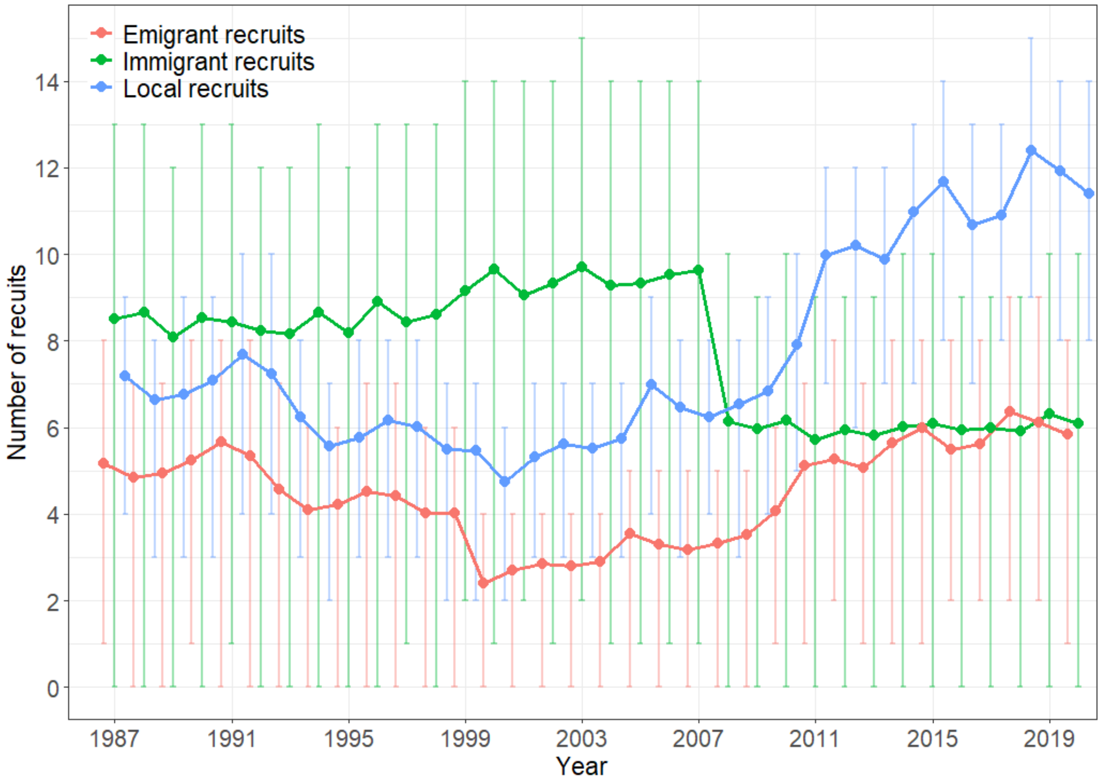

Figure 5. Numbers of local, emigrant, and immigrant recruits in the study population (1987-2020). Points indicate posterior mean values and error bars indicate 90% credible intervals.

Visual patterns in Figure 6 suggest that the balance between births and deaths showed a larger influence on average population growth rates and sink-source status than the balance between the numbers of immigrants and emigrants. Years with larger birth surpluses showed larger population growth rates and higher probabilities for the population to operate as a source.

<u>Sink-source status</u>

The sink-source status of the population varied between years, yet the population was most often classified as a sink between 1987 and 2008: the sink-source estimator C^r during these years was 0.975 on average (values smaller than 1 indicate that the population is a sink), and the average probability of being a source (i.e., percentage of posterior samples in which C^r was larger than 1) was estimated at 35%. Instead, between

2008 and 2020, average C^r was 1.030, and the average probability of being a source was 63% (Figure 7).

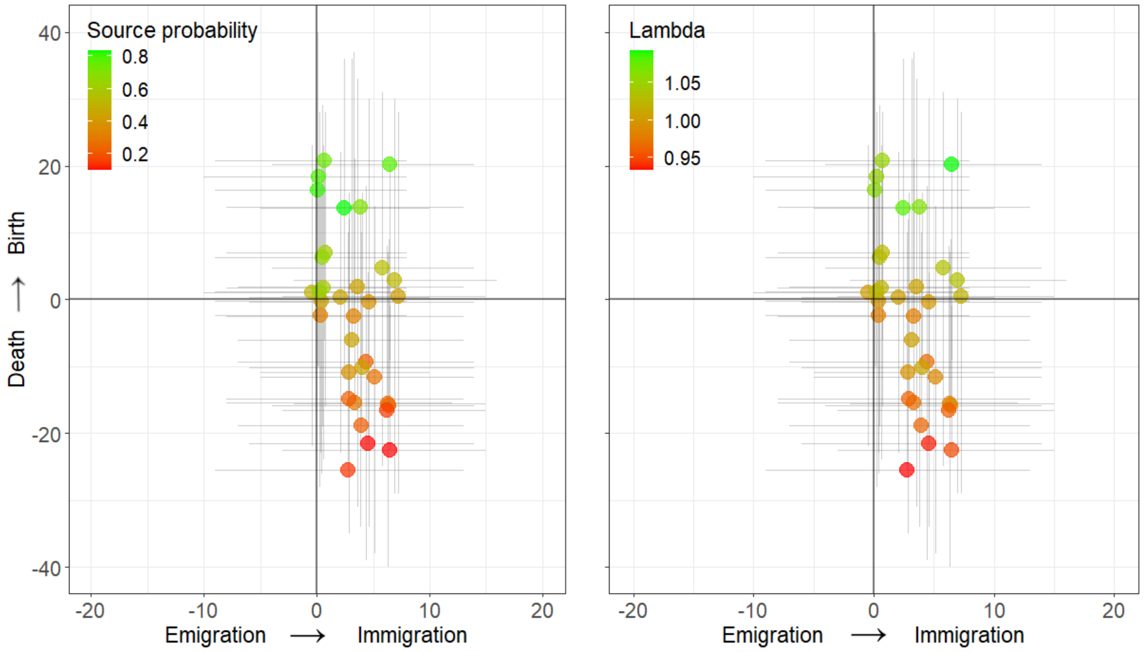

Figure 6. Yearly posterior mean difference between births and deaths (Y) vs. posterior mean difference between emigration and immigration (X). Grey lines indicate 90% credible intervals of the difference between births and deaths (vertical) and between emigration and immigration (horizontal). Point colours indicate average source probabilities (left panel) and population growth rates (right panel).

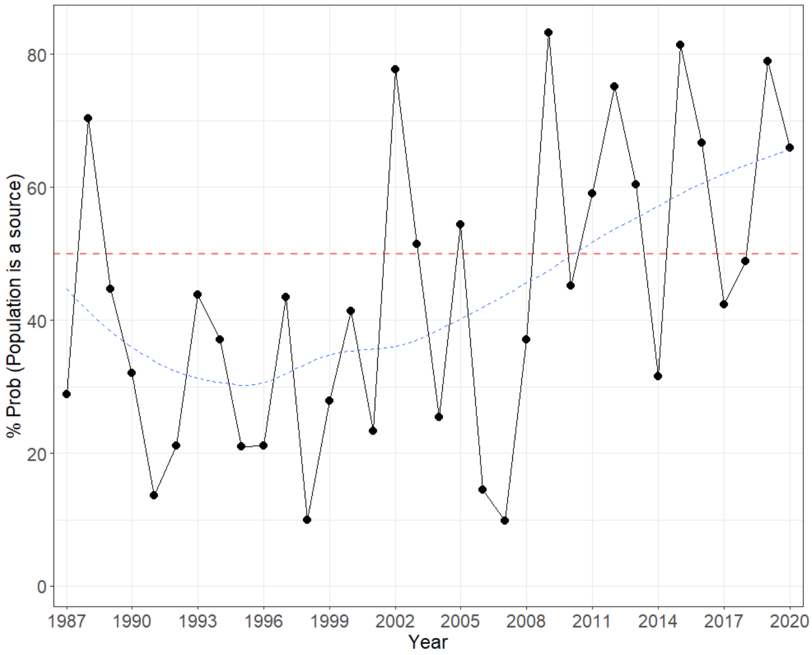

Figure 7. Yearly probabilities of the study population being a source (i.e., $C^r>1$). The red dashed line indicates the 50% probability threshold, below which the population is more likely to operate as a sink. The dashed blue line indicates the smoothed sink-source trend of the population along time and was fitted using local polynomial regression.

Estimation of demographic parameters

Breeder survival showed large interannual variation (Figure 8) with yearly average values around 0.85 and 0.95 and a trend for a slight increase along time (i.e., from 0.887, 90%CRI = 0.809-0.974 for the period 1986-1999, to 0.907, 0.841-0.975 for 2008-2020). Non-breeder survival probabilities progressively increased along time (Figure 9). Probabilities were 0.473 (0.341-0.602) for juveniles and 0.494 (0.335-653) for the rest of ages in 1986-1999. Instead, in 2000-2007, probabilities were estimated at 0.481 (0.368-0.593) for juveniles, 0.57 (0.507-0.634) for immatures and subadults, and 0.870 (0.831-0.909) for adults. In the last period, 2008-2020, estimates were the largest on average, with 0.657 (0.582-0.730) for juveniles, 0.715 (0.646-0.780) for immatures and subadults, and 0.866 (0.768-0.944) for adults.

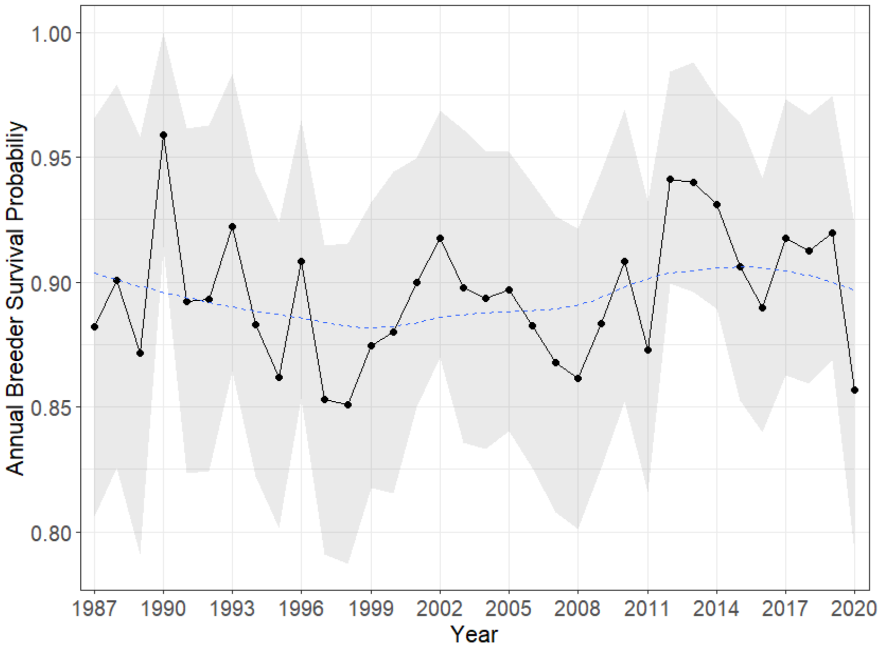

Figure 8. Yearly breeder survival probabilities (1987-2020). Points show posterior means and shaded areas show 90% credible intervals. The dashed blue line indicates the smoothed breeder survival trend along time and was fitted using local polynomial regression.

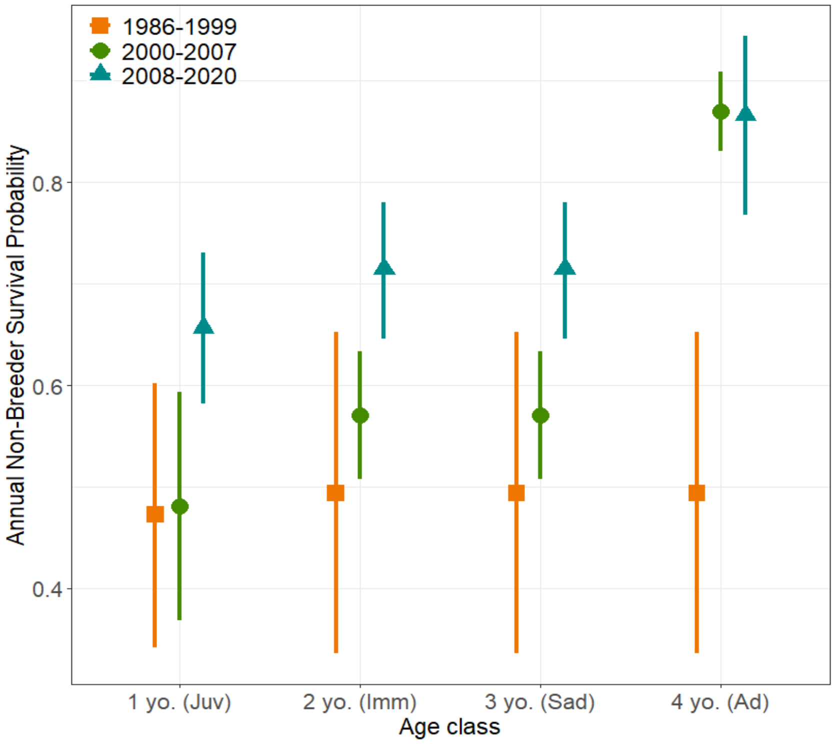

Figure 9. Posterior mean (points) and 90% credible intervals (error lines) of annual non-breeder survival estimates by period and age class. Abbreviations "yo"., "Juv", "Imm", "Sad", and "Ad" stand for "years old", "juveniles", "immatures", "subadults", and "adults" respectively.

Permanent emigration probabilities showed a decreasing trend from 0.407 (0.246-0.577) in 1986-1999 to 0.340 (0.258 – 0.410) in 2008-2020. Probabilities of recruitment to the breeding population generally decreased along time (Figure 10). Immature recruitment was estimated at 0.274 (0.091-0.442), 0.176 (0.083-0.270), and 0.171 (0.114-0.236) respectively for the periods 1986-1999, 2000-2007, and 2008-2020. For subadults, recruitment was estimated at 0.746 (0.482 – 0.999), 0.603 (0.392-0.816), and 0.499 (0.383-0.617) respectively, and for adults, it was estimated at 0.746 (0.482-0.999), 0.110 (0.020-0.193), and 0.222 (0.130-0.330) respectively. Productivity showed a steady declining trend along time (Figure 11): the estimated number of raised fledglings peaked at 1.408 (1.016-1.800) in 1987, and progressively declined to values around 0.9 on average (e.g., 0.869, 0.659-1.077, in 2020).

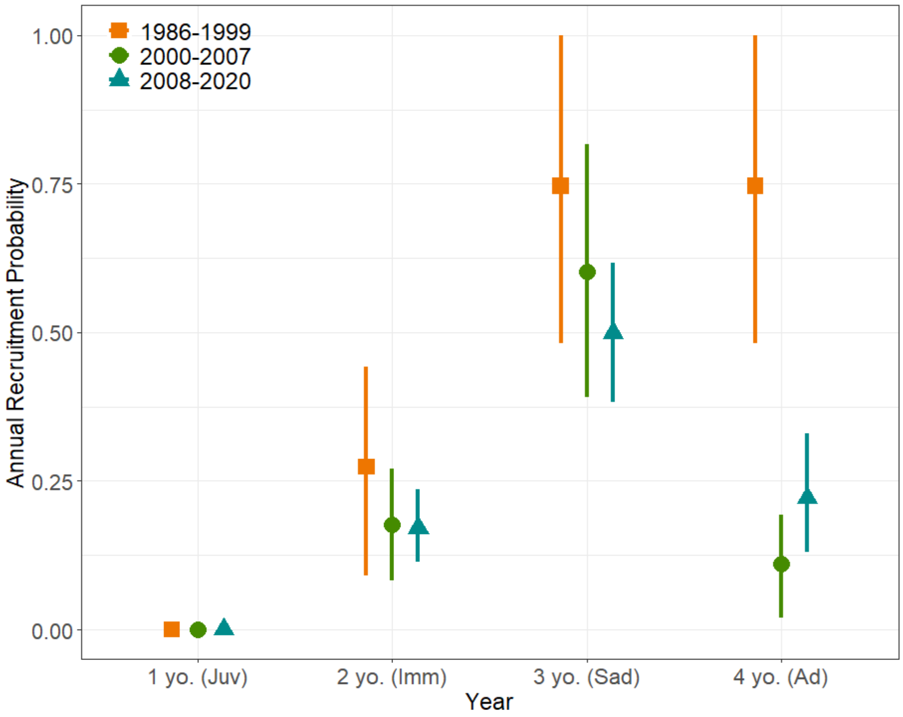

Figure 10. Posterior mean (points) and 90% credible intervals (error lines) of annual probabilities of recruitment to the breeding population by period and age class. Abbreviations “yo”., “Juv”, “Imm”, “Sad”, and “Ad” stand for “years old”, “juveniles”, “immatures”, “subadults”, and “adults” respectively.

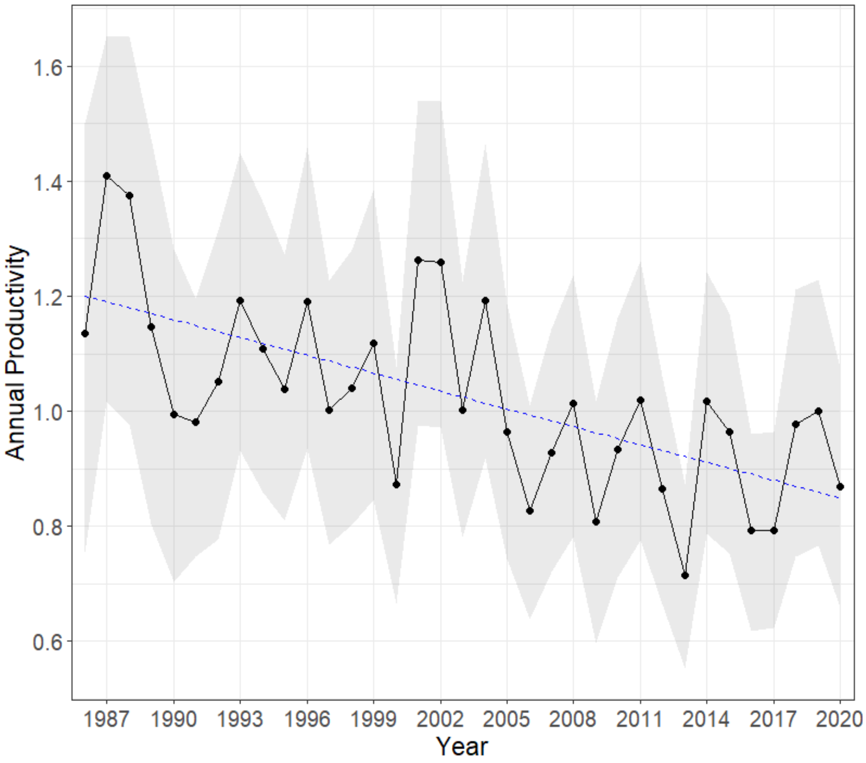

Figure 11. Yearly productivity rates (1986-2020). Points show posterior means and shaded areas show 90% credible intervals. The dashed blue line indicates the average linear productivity trend along time.

The population growth rate showed the largest sensitivity (0.816, 0.706-0.945) and elasticity (0.730, 0.615-0.870) to breeder survival (Figure 12). Non-breeder survival showed considerably lower values, with sensitivity estimated at 0.356 (0.182-0.497) and elasticity at 0.227 (0.086-0.342). Productivity showed the smallest sensitivity (0.076, 0.052-0.106) and elasticity (0.077, 0.054-0.101). A detailed report of parameters obtained in multievent replacement models and multistate models (e,g,, recovery, resighting, fidelity probabilities) is provided at Appendix S3 and Tables S2 to S4 therein.

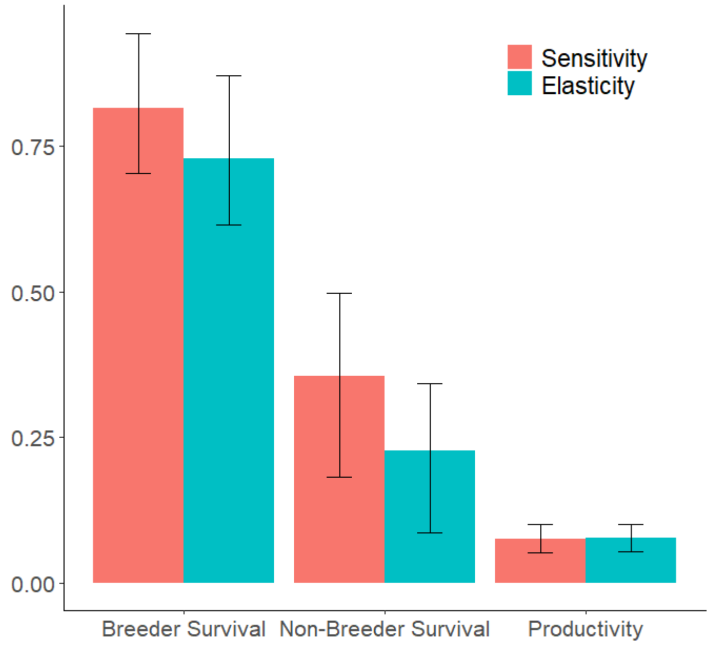

Figure 12. Posterior means and 90% credible intervals of sensitivity and elasticity for survival and productivity estimates. The calculations were performed using perturbation analysis.

Discussion

Modelling all processes that cause population gains (i.e., birth and immigration) and losses (i.e., death and emigration) together with stage-structured demographic parameters and population sizes along time may be fundamental for a deep understanding of the complex dynamics of long-lived populations. We designed a spatially-explicit Integrated Population Model (SEIPM) to model the long-term birth, immigration, death, and emigration processes along with key vital rates, stage-structured population sizes, and sink-source dynamics in a threatened population of a long-lived raptor, the Bonelli's eagle in Catalonia (W Europe, 1986-2020). Using this approach, we characterized the long-term dynamics of this population encompassing different phases of population growth. Overall, the present study illustrates the potential of SEIPMs at describing long-lived population dynamics from a novel perspective and at a finer scale.

In the study population, the magnitude of birth and death processes (100-200 individuals/year) was considerably larger than that of emigration and immigration (10-20 ind./year). This fact suggests that the equilibrium between births and deaths is the most influential factor for population growth. However, differences between births and deaths at most years of the study were small, i.e., 5-10 individuals on average. Importantly, differences of such magnitude were sufficient to lead to a considerable population decline and a relatively rapid recovery afterwards. While this may be expected in long-lived species due to their slow life paces, such differences may be difficult to detect even with sophisticated analytical methods given their small scale (Saether & Bakke, 2000). This fact may illustrate the fine-scale level at which population dynamics are driven in these species. In any case, the apparently lower influence of migration processes on population growth is an interesting finding considering the generally large natal dispersal patterns of the study species and its connectivity with neighbouring populations (Hernández-Matías et al., 2010, 2013; Cadahía et al., 2010; Badia-Boher et al., 2023). Importantly, in the study species, permanent emigration and immigration operate at the time of recruitment to the breeding population. As a result, while the impact of these processes on the total population may be modest, a more important effect could be found on the dynamics of the breeding population. Immigration tended to be the largest source of recruits during most of the study period, especially in phases of decline and stability of the breeder population (i.e., 1986-2008). Thus, immigration probably prevented larger breeder declines during these years. Interestingly, these findings are similar to those of Lieury et al. (2016) for the neighbouring Bonelli's eagle population in France, where immigrants were the main source of recruits and softened breeder population declines during the same period. This fact may again underline the similarities between the dynamics of both populations along time (see *Methods*).

Interestingly, the yearly estimates of birth and death numbers showed a progressive decline from the beginning to the end of the study. The decline in the number of deaths was associated to large increases in non-breeder survival and a trend for a slight increase in breeder survival. The most probable reason for such increases was the implementation of power line retrofitting actions both in breeding territories and non-breeder dispersal areas aimed at reducing electrocution and collision risks (Hernández-Matías et al., 2015, 2020). As in many raptor species, power line infrastructure was a main cause of mortality in the study population, and management actions aimed at its mitigation are known to be potentially central to halt population declines (Hernández-Matías et al., 2015; Chevalier et al., 2015; Ogada et al., 2016, Badia-Boher et al., 2019). Besides, sensitivity and elasticity analyses showed that breeder survival was by far the largest driver of the population's growth rate, with an approximate two-to-three-fold impact compared to non-breeder survival. This result matches those of other studies conducted in this and other long-lived species (Hernández-Matías et al., 2013; Chevallier et al., 2015; Margalida et al., 2020), and suggest that even small variations in breeder survival may have large implications for the dynamics of the study population (see Hernández-Matías et al., 2013). For instance, in the neighbouring Bonelli's eagle population in France, an increase by 0.03 in adult survival already had the capacity to revert population decline (Chevallier et al., 2015). Even though our breeder survival estimation was quite precise, such small increases may not be reliably detected with the present uncertainty associated with our estimates. Besides, also in the French population, non-breeder survival needed to increase by 0.14. This threshold was largely overcome from 1986-1999 to 2008-2020 for all age classes in the study population. Hence, non-breeder survival probably had a central role in the observed recovery of the population.

Our long-term sink-source assessments showed that the study population progressively switched from a frequent sink in the 1980s, 1990s, and 2000s, to a frequent source status in the 2010s. To our knowledge, this could be one of the first evidences of a long-term transition from a sink to a source functioning in a long-lived species population based on actual data. This may contrast with prior knowledge suggesting that despite variations in their strengths over time, the overall status of populations as sinks or sources may be strongly conserved (Guo et al., 2005; Heinrichs et al., 2019a). Yet, it is important to consider that the population was either estimated as a weak sink or a weak source in most years (i.e., average values mostly varied between 0.95 and 1.05). This weak status could have facilitated the observed sink-source transition, which might be more unlikely for populations acting as strong sinks or sources (Lieury et al., 2016; Heinrichs et al., 2019a). Besides, the visual trends of Figure 6 suggest that the balance between births and deaths in the study population influenced sink-source status more than the balance between emigrants and immigrants. This finding supports the conclusions of Heinrichs et al. (2019a), who suggested that changes in inter-population movements had a weak ability to modify sink-source dynamics in spatially-structured populations, while changes in local abundances could have a larger influence. In this respect, the switch in sink-source trends occurred along with increments in the population in the 2010s decade. These increases were likely caused by increases in survival, which were probably the result of management action. This may support the idea that conservation action may promote changes in the magnitudes of sinks and sources, and even in sink-source status (Heinrichs et al., 2019a; this study).

Furthermore, our assessment of the population as a frequent sink in the 1990s and early 2000s coincide with the results of the spatial PVAs conducted for the whole western European Bonelli's eagle range by Hernández-Matías et al. (2013). The conclusions of that work suggested that source core areas in the south of the range contributed to sinks in the north (including Catalonia). Interestingly, the observed sink-source changes of the Catalan population, along with the suggestions that the French population might be functioning as a weaker sink in recent times may indicate some flexibility in the global sink-source patterns of spatially-structured populations (Lieury et al., 2016; Heinrichs et al., 2016a). Variations in the Catalan and French populations have been accompanied with further population growth changes in other areas in the last decades: increases in the numbers of breeding pairs in northern populations that were previously decreasing (i.e., Castilla y Leon region in the northwest and Catalonia and France in the northeast), considerable decreases in previously stable central-eastern populations (i.e., Valencia region), and sustained decreases in other northern populations (del Moral, 2006; del Moral & Molina, 2018). These changed patterns may be worth an updated evaluation, which may help at further understanding how, why, and how much source-sink dynamics may vary in the long-term in whole spatially-structured long-lived populations.

The estimated population decline between the early 1990s and the early 2000s was especially visible in the breeding population, which lost ca. 22% of the initial size in 15 years. At that phase, the floater population was estimated as practically drained. The low non-breeder survival estimates for that period probably prevented the accumulation of the sufficient floater base to buffer breeder deaths, ultimately causing the observed decline. This finding may be one of the first estimations from wild populations to support the simulation works of Penteriani et al. (2005, 2008), which suggested that exhaustions in the floater population could result into sharp breeding population declines. During this same period, large recruitment probabilities were estimated, suggesting a large availability of empty breeding spots in territories (Ferrer et al., 2004; Votier et al., 2008). This result adds to previous findings showing that increases in recruitment rates may be a buffer mechanism to halt or soften breeder population declines in territorial populations (Muths et al., 2011; Penteriani et al., 2011). The subsequent stabilization (2000 – 2010) and increase (2011-2020) of the breeding populations occurred in parallel to large improvements in non-breeder survival. The floater population considerably increased during these periods, with a substantial accumulation of non-breeding adults, and coinciding with a decrease in recruitment probabilities for all ages. Altogether, these findings suggest that breeding opportunities in the population became limited due to the breeding and floater population increases (Hunt, 1998; Ferrer et al., 2004; Penteriani et al., 2011). Importantly, in territorial populations, large accumulations of floaters may promote increments and range expansions in the breeding population via the colonization of new territories (Hunt, 1998). In the case of our study, the breeder population increase between 2001 (minimum) and 2020 (maximum) implied the progressive colonization of 17 new or previously abandoned breeding territories. Of these, 12 territories were occupied between 2012 and 2020, coinciding with the largest accumulations of floaters. Furthermore, increases in the floater population occurred along with increases in the number of emigrants. Because recruitment and permanent emigration in the study species are intrinsically linked, increases in the number of individuals ready to recruit (i.e., floaters) may result into larger numbers of emigrants, thus contributing not only to the local population, but also to the neighbouring ones.

Floaters are often described as a double-edged sword for population regulation, with negative effects through increased competition with breeders and positive effects for population stability via the buffer effect (López-Sepulcre & Kokko, 2005; Penteriani et al., 2011). A popular metric to assess the resilience of breeder populations is the floater-to-breeder ratio $\frac{N_F}{N_B}$, which some authors defined as ideally 1 for optimal population stability (Newton, 1988; Hunt, 1998; Katzenberger et al., 2021). In the study population, such ratio was practically 0 at the beginning of the study. In 2020, when the floater population reached its maximum size, the ratio was still considerably far from 1 (i.e., 0.162, 90%CRI = 0.055-0.263). Even with this relatively low ratio, recent field observations suggest that the existing pool of floaters might already be contributing to increased competition with breeders. Namely, floater interferences in breeding territories are increasingly observed during territory watching campaigns, while they were extremely rare in past decades (own data; Penteriani et al., 2011). Frequent interferences are known to potentially cause declines in fecundity rates, and thus may be a potential explanation for the estimated decrease in productivity simultaneous to the increase in floater numbers in our study (Mougeot et al., 2002; Bretagnolle et al., 2008; but see Ferrer et al., 2015). In any case, the available evidence suggests that these potentially negative effects are unlikely to offset the positive effects of floater increases for population stability (Newton, 1988; Hunt, 1998; Penteriani et al., 2011).

In our study, immigration was estimated as a hidden parameter with no explicit data, as is commonplace in integrated population models (Abadi et al., 2011; Schaub & Fletcher, 2015). This type of estimation assumes that information on immigration is contained at the difference between the observed population counts and the estimated population numbers by the model. Because this difference may be caused by factors other than immigration, this type of estimation could be biased in some scenarios. For instance, if models ignore processes that add or remove individuals in a population (i.e., birth, emigration, death, tag loss), immigration as a hidden parameter may end up reflecting any of these parameters instead of true immigration (Riecke et al., 2019; Plard et al., 2021). In our study, we carefully accounted for all processes leading to individual gain and loss (i.e., birth, death and emigration processes along with immigration). Additionally, we accounted for tag loss whenever present (i.e., in the 1986-1999 CMR dataset). Furthermore, our immigration and sink-source estimates matched the results of Hernández-Matías et al. (2013) for the 1990-2005 period, which showed that immigration was the main migration process in the population and the population was a sink. For all these reasons, we are confident that our estimation of immigration may be reliable.

Overall, the integration of spatially-explicit capture-mark-recapture models into SEIPMs offers a compelling framework to assess population dynamics from a more complete perspective. An important advantage of SEIPMs is their ease at estimating sink-source dynamics, which may facilitate further studies of their long-term variability, environmental, and demographic drivers. Given the central role of source-sink dynamics for conservation, such knowledge could be of great use to design more effective management actions for spatially-structured populations and predict potential changes in sink-source status and strength (Heinrichs et al., 2019a). In addition, the explicit modelling of emigration in these models may also permit a more complete understanding of the role of this process for population dynamics. So far, immigration has been considered in several IPMs, revealing its central yet previously unknown role in several populations (e.g., Schaub et al., 2010; Altwegg et al., 2014; Lieury et al., 2016). However, the available evidence on emigration is weaker because this process has often been explicitly incorporated using apparent survival estimates and not treated as a differentiated process. Hence, we hope that further research based on spatially-explicit IPMs can shed light on the demographic role and magnitude of this process. Overall, we believe that the flexibility and potentialities of spatially-explicit IPMs can contribute to addressing historical knowledge gaps in the study of animal demography and help at a more effective implementation of conservation action.

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Data availability statement

The code used in this study is available in the figshare repository, https://figshare.com/s/5526a8866457a8bfa78e .

Additional information

The authors declare no competing interests.

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Supplementary Material S1 – State-transition and observation matrices of the capture-mark-recapture models used in the spatially-explicit Integrated Population Model

1) 1986-1999 state-transition and observation matrices

State codes:

- ANB-PM: Alive as non-breeder wearing PVC and metal rings.
- ANB-P: Alive as non-breeder wearing PVC ring only.
- ANB-M: Alive as non-breeder wearing metal ring only.
- AB-PM: Alive as breeder wearing PVC and metal rings.
- AB-P: Alive as breeder wearing PVC ring only.
- AB-M: Alive as breeder wearing metal ring only.
- DNB-PM: Dead as non-breeder wearing PVC and metal rings.
- DNB-P: Dead as non-breeder wearing PVC ring only.
- DNB-M: Dead as non-breeder wearing metal ring only.
- DB-PM: Dead as breeder wearing PVC and metal rings
- DB-P: Dead as breeder wearing PVC ring only
- DB-M: Dead as breeder wearing metal ring only
- AS: Absorbing State

Parameters

- S: True survival
- ϒ: Recruitment to the breeding population
- lp: Loss of PVC ring
- lm: Loss of metal ring
- Pd: Joint estimation parameter
- r: Recovery

Subindices

- a: Age
- i: Individual
- t: Time
- NB: Non-breeder
- B: Breeder
- $terr$: Territory

Because the state transition matrix would be too long to be shown (i.e., 13x13 with multiple parameters), we decomposed it into the different transitions from state at *t* to state at $t+1$.

1986-1999 State-transition matrix probabilities (State at t → State at t+1):

- P(ANB-PM → ANB-PM) = $S_{NB_a} * (1-\gamma_a) * (1-lp) * (1-lm)$
- P(ANB-PM → ANB-P) = $S_{NB_a} * (1-\gamma_a) * (1-lp) * lm$
- P(ANB-PM → ANB-M) = $S_{NB_a} * (1-\gamma_a) * lp * (1-lm)$
- P(ANB-PM → AB-PM) = $S_{NB_a} * \gamma_a * P_{d_i} * (1-lp) * (1-lm)$
- P(ANB-PM → AB-P) = $S_{NB_a} * \gamma_a * P_{d_i} * (1-lp) * lm$
- P(ANB-PM → AB-M) = $S_{NB_a} * \gamma_a * P_{d_i} * lp * (1-lm)$
- P(ANB-PM → DNB-PM) = $\left(1-S_{NB_a}\right) * (1-\gamma_a) * (1-lp) * (1-lm) * r$
- P(ANB-PM → DNB-P) = $\left(1-S_{NB_a}\right) * (1-\gamma_a) * (1-lp) * lm * r$
- P(ANB-PM → DNB-M) = $\left(1-S_{NB_a}\right) * (1-\gamma_a) * lp * (1-lm) * r$
- P(ANB-PM → DB-PM) = $\left(1-S_{NB_a}\right) * \gamma_a * P_{d_i} * (1-lp) * (1-lm) * r$
- P(ANB-PM → DB-P) = $\left(1-S_{NB_a}\right) * \gamma_a * P_{d_i} * (1-lp) * lm * r$
- P(ANB-PM → DB-M) = $\left(1-S_{NB_a}\right) * \gamma_a * P_{d_i} * lp * (1-lm) * r$
- P(ANB-PM → AS) = $\left(\left(1-S_{NB_a}\right) * (1-r)\right) + \left(S_{NB_a} * lm * lp\right) + \left(\left(1-S_{NB_a}\right) * lm * lp\right) + \left(S_{NB_a} * \gamma_a * \left(1-P_{d_i}\right)\right) + \left((1-S_{NB_a}) * \gamma_a * \left(1-P_{d_i}\right)\right)$

- P(ANB-P → ANB-PM) = 0
- P(ANB-P → ANB-P) = $S_{NB_a} * (1-\gamma_a) * (1-lp)$
- P(ANB-P → ANB-M) = 0
- P(ANB-P → AB-PM) = 0
- P(ANB-P → AB-P) = $S_{NB_a} * \gamma_a * P_{d_i} * (1-lp)$
- P(ANB-P → AB-M) = 0
- P(ANB-P → DNB-PM) = 0
- P(ANB-P → DNB-P) = $\left(1-S_{NB_a}\right) * (1-\gamma_a) * (1-lp) * r$
- P(ANB-P → DNB-M) = 0
- P(ANB-P → DB-PM) = 0
- P(ANB-P → DB-P) = $\left(1-S_{NB_a}\right) * \gamma_a * P_{d_i} * (1-lp) * r$
- P(ANB-P → DB-M) = 0
- P(ANB-P → AS) = $\left(\left(1-S_{NB_a}\right) * (1-r)\right) + \left(S_{NB_a} * lp\right) + \left(\left(1-S_{NB_a}\right) * lp\right) + \left(S_{NB_a} * \gamma_a * \left(1-P_{d_i}\right)\right) + \left((1-S_{NB_a}) * \gamma_a * \left(1-P_{d_i}\right)\right)$

- P(ANB-M → ANB-PM) = 0
- P(ANB-M → ANB-P) = 0
- P(ANB-M → ANB-M) = $S_{NB_a} * (1-\gamma_a) * (1-lm)$
- P(ANB-M → AB-PM) = 0
- P(ANB-M → AB-P) = 0
- P(ANB-M → AB-M) = $S_{NB_a} * \gamma_a * P_{d_i} * (1-lm)$
- P(ANB-M → DNB-PM) = 0
- P(ANB-M → DNB-P) = 0
- P(ANB-M → DNB-M) = $\left(1-S_{NB_a}\right) * (1-\gamma_a) * (1-lm) * r$
- P(ANB-M → DB-PM) = 0
- P(ANB-M → DB-P) = 0
- P(ANB-M → DB-M) = $\left(1-S_{NB_a}\right) * \gamma_a * P_{d_i} * (1-lm) * r$

- P(ANB-M → AS) = $\left(\left(1-S_{NB_a}\right)*(1-r)\right)+\left(S_{NB_a}*lm*lp\right)+\left(\left(1-S_{NB_a}\right)*lm*lp\right)+\left(S_{NB_a}*\ \gamma_a*\left(1-P_{d_i}\right)\right)+\ \left((1-S_{NB_a})*\ \gamma_a*\left(1-P_{d_i}\right)\right)$

- P(AB-PM → ANB-PM) = 0
- P(AB-PM → ANB-P) = 0
- P(AB-PM → ANB-M) = 0
- P(AB-PM → AB-PM) = $S_B\ *\ (1-lp)*(1-lm)$
- P(AB-PM → AB-P) = $S_B\ *\ (1-lp)*lm$
- P(AB-PM → AB-M) = $S_B\ *\ lp*(1-lm)$
- P(AB-PM → DNB-PM) = 0
- P(AB-PM → DNB-P) = 0
- P(AB-PM → DNB-M) = 0
- P(AB-PM → DB-PM) = $(1-S_B)*(1-lp)*(1-lm)*r$
- P(AB-PM → DB-P) = $(1-S_B)*\ (1-lp)*lm*r$
- P(AB-PM → DB-M) = $(1-S_B)*lp*(1-lm)*r$
- P(AB-PM → AS) = $\left((1-S_B)*(1-r)\right)+(S_B\ *lm*lp)+\left((1-S_B)*lm*lp\right)$

- P(AB-P → ANB-PM) = 0
- P(AB-P → ANB-P) = 0
- P(AB-P → ANB-M) = 0
- P(AB-P → AB-PM) = 0
- P(AB-P → AB-P) = $S_B\ *\ (1-lp)$
- P(AB-P → AB-M) = 0
- P(AB-P → DNB-PM) = 0
- P(AB-P→ DNB-P) = 0
- P(AB-P → DNB-M) = 0
- P(AB-P → DB-PM) = 0
- P(AB-P → DB-P) = $(1-S_B)*\ (1-lp)*r$
- P(AB-P → DB-M) = 0
- P(AB-P → AS) = $\left((1-S_B)*(1-r)\right)+(S_B\ *lp)+\left((1-S_B)*lp\right)$

- P(AB-M → ANB-PM) = 0
- P(AB-M → ANB-P) = 0
- P(AB-M → ANB-M) = 0
- P(AB-M → AB-PM) = 0
- P(AB-M → AB-P) = 0
- P(AB-M → AB-M) = $S_B\ *(1-lm)$
- P(AB-M → DNB-PM) = 0
- P(AB-M → DNB-P) = 0
- P(AB-M → DNB-M) = 0
- P(AB-M → DB-PM) = 0
- P(AB-M → DB-P) = 0
- P(AB-M → DB-M) = $(1-S_B)*(1-lm)*r$
- P(AB-M → AS) = $\left((1-S_B)*(1-r)\right)+(S_B\ *lm)+\left((1-S_B)*lm\right)$

- P(DNB-PM → ANB-PM) = 0
- P(DNB-PM → ANB-P) = 0
- P(DNB-PM → ANB-M) = 0
- P(DNB-PM → AB-PM) = 0
- P(DNB-PM → AB-P) = 0
- P(DNB-PM → AB-M) = 0
- P(DNB-PM → DNB-PM) = 0
- P(DNB-PM → DNB-P) = 0
- P(DNB-PM → DNB-M) = 0
- P(DNB-PM → DB-PM) = 0
- P(DNB-PM → DB-P) = 0
- P(DNB-PM → DB-M) = 0
- P(DNB-PM → AS) = 1

- P(DNB-P → ANB-PM) = 0
- P(DNB-P → ANB-P) = 0
- P(DNB-P → ANB-M) = 0
- P(DNB-P → AB-PM) = 0
- P(DNB-P → AB-P) = 0
- P(DNB-P → AB-M) = 0
- P(DNB-P → DNB-PM) = 0
- P(DNB-P → DNB-P) = 0
- P(DNB-P → DNB-M) = 0
- P(DNB-P → DB-PM) = 0
- P(DNB-P → DB-P) = 0
- P(DNB-P → DB-M) = 0
- P(DNB-P → AS) = 1

- P(DNB-M → ANB-PM) = 0
- P(DNB-M → ANB-P) = 0
- P(DNB-M → ANB-M) = 0
- P(DNB-M → AB-PM) = 0
- P(DNB-M → AB-P) = 0
- P(DNB-M → AB-M) = 0
- P(DNB-M → DNB-PM) = 0
- P(DNB-M → DNB-P) = 0
- P(DNB-M → DNB-M) = 0
- P(DNB-M → DB-PM) = 0
- P(DNB-M → DB-P) = 0
- P(DNB-M → DB-M) = 0
- P(DNB-M → AS) = 1

- P(DB-PM → ANB-PM) = 0
- P(DB-PM → ANB-P) = 0
- P(DB-PM → ANB-M) = 0
- P(DB-PM → AB-PM) = 0
- P(DB-PM → AB-P) = 0
- P(DB-PM → AB-M) = 0
- P(DB-PM → DNB-PM) = 0
- P(DB-PM → DNB-P) = 0
- P(DB-PM → DNB-M) = 0
- P(DB-PM → DB-PM) = 0
- P(DB-PM → DB-P) = 0
- P(DB-PM → DB-M) = 0
- P(DB-PM → AS) = 1

- P(DB-P → ANB-PM) = 0
- P(DB-P → ANB-P) = 0
- P(DB-P → ANB-M) = 0
- P(DB-P → AB-PM) = 0
- P(DB-P → AB-P) = 0
- P(DB-P → AB-M) = 0
- P(DB-P → DNB-PM) = 0
- P(DB-P → DNB-P) = 0
- P(DB-P → DNB-M) = 0
- P(DB-P → DB-PM) = 0
- P(DB-P → DB-P) = 0
- P(DB-P → DB-M) = 0
- P(DB-P → AS) = 1

- P(DB-M → ANB-PM) = 0
- P(DB-M → ANB-P) = 0
- P(DB-M → ANB-M) = 0
- P(DB-M → AB-PM) = 0
- P(DB-M → AB-P) = 0
- P(DB-M → AB-M) = 0
- P(DB-M → DNB-PM) = 0
- P(DB-M → DNB-P) = 0
- P(DB-M → DNB-M) = 0
- P(DB-M → DB-PM) = 0
- P(DB-M → DB-P) = 0
- P(DB-M → DB-M) = 0
- P(DB-M → AS) = 1

- P(AS → ANB-PM) = 0
- P(AS → ANB-P) = 0
- P(AS → ANB-M) = 0
- P(AS → AB-PM) = 0
- P(AS → AB-P) = 0
- P(AS → AB-M) = 0
- P(AS → DNB-PM) = 0
- P(AS → DNB-P) = 0
- P(AS → DNB-M) = 0

- P(AS → DB-PM) = 0
- P(AS → DB-P) = 0
- P(AS → DB-M) = 0
- P(AS → AS) = 1

1986-1999 observation matrix:

$$
\begin{array}{r|ccccccccccccc|}
\mathbf{t\,/\,t} & \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} & \mathbf{6} & \mathbf{7} & \mathbf{8} & \mathbf{9} & \mathbf{10} & \mathbf{11} & \mathbf{12} & \mathbf{13} \\
\textbf{ANB-PM} & p_{NB} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{NB} \\
\textbf{ANB-P} & 0 & p_{NB} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{NB} \\
\textbf{ANB-M} & 0 & 0 & p_{NB} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{NB} \\
\textbf{AB-PM} & 0 & 0 & 0 & p_{B} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{B} \\
\textbf{AB-P} & 0 & 0 & 0 & 0 & p_{B} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{B} \\
\textbf{AB-M} & 0 & 0 & 0 & 0 & 0 & p_{B} & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_{B} \\
\textbf{DNB-PM} & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
\textbf{ANB-P} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
\textbf{ANB-M} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
\textbf{AB-PM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
\textbf{AB-P} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
\textbf{AB-M} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
\textbf{AS} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}
$$

Figure S1. Observation matrix of the 1986-1999 multistate model. Rows indicate the states of the individual i at time t, columns indicate observations/events of individuals i at time t. Observation codes 1 to 12 correspond to the probability of observing an individual in each of the states sorted in the same order (ANB-PM to AB-M). Observation code 13 stands for “not seen”. The matrix includes the parameters P_{NB} (non-breeder recapture) and P_{B} (breeder recapture).

2) 2008-2020 state-transition and observation matrices

$$\begin{array}{c|ccccc} t\,/\,t{+}1 & \textbf{ANB} & \textbf{AB} & \textbf{DNB} & \textbf{DB} & \textbf{AS} \\ \hline \textbf{ANB} & (S_{NB_a} * (1-\gamma_a)) & (S_{NB_a} * \gamma_a * P_{d_i}) & \left((1-S_{NB_a}\right) * \left(1-\gamma_a\right) * r_{NB}) & ((1-S_{NB_a}) * \left(\gamma_a\right) * r_B) & *_A \\ \textbf{AB} & 0 & S_B & 0 & (1-S_B) * r_B & (1-S_B) * (1-r_B) \\ \textbf{DNB} & 0 & 0 & 0 & 0 & 1 \\ \textbf{DB} & 0 & 0 & 0 & 0 & 1 \\ \textbf{AS} & 0 & 0 & 0 & 0 & 1 \end{array}$$

$$*\text{A: } \left((1-S_{NB_a}) * (1-\gamma_a) * (1-r_{NB})\right) + \left(S_{NB_a} * \gamma_a * (1-P_{d_i})\right) + \left((1-S_{NB_a}) * \gamma_a * (1-P_{d_i})\right) + ((1-S_{NB_a}) * \gamma_a * (1-r_B) * P_{d_i})$$

Figure S2. State transition matrix of the 2008-2020 multistate model. Rows indicates the state of individuals i at time t, columns indicate states at time t+1. The matrix includes the parameters S_{NB} (non-breeder survival), S_B (breeder survival), γ (recruitment to the breeding population), P_d (joint-estimation parameter), and r (probability of encountering a dead marked individual that was either non-breeder, r_{NB}, or breeder, r_B). Subindices indicate age ($_a$) and individual ($_i$). States are Alive as Non-Breeder (ANB), Alive as Breeder (AB), Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Due to the length of the first absorbing state expression (i.e., transition from ANB in t to AS in t+1), we wrote this expression outside the matrix ($*_A$).

$$\begin{array}{c|ccccc} t\,/\,t & \textbf{1} & \textbf{2} & \textbf{3} & \textbf{4} & \textbf{5} \\ \hline \textbf{ANB} & p_{NB} & 0 & 0 & 0 & 1-p_{NB} \\ \textbf{AB} & 0 & p_{B1_{terr_i},t} * \left(1-covpb_{i,t}\right) + p_{B_t} * covpb_{i,t} & 0 & 0 & 1-p_B \\ \textbf{DNB} & 0 & 0 & 1 & 0 & 0 \\ \textbf{DB} & 0 & 0 & 0 & 1 & 0 \\ \textbf{AS} & 0 & 0 & 0 & 0 & 1 \end{array}$$

Figure S3. Observation matrix of the 2008-2020 multistate model. Rows indicate the states of the individual i at time t, columns indicate observations/events of individuals i at time t. The matrix includes the parameters p_{NB} (non-breeder recapture), p_{B1} (probability of being observed for the first time once the individual has become breeder), and p_B (breeder recapture for those individuals observed as breeders at least once already), and the binary covariate covpb, which assigns either p_{B1} or p_B as observation parameters to deal with detection heterogeneity in breeder detection probabilities. States are Alive as Non-Breeder (ANB), Alive as Breeder, Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Observations/Events are Alive as Non-Breeder (1), Alive as Breeder (2), Recovered as Non-Breeder (3), Recovered as Breeder (4) and Unobserved (5).

3) 1986-2020 Multievent data for the estimation of breeder survival

$$
\begin{array}{c|cccccc}
t / t+1 & \text{F} & \text{A-E} & \text{M-E} & \text{F} & \text{A-R} & \text{M-R} \\
\hline
\text{E} & 1-c & 0 & 0 & c & 0 & 0 \\
\text{A-E} & 1-c & 0 & 0 & c & 0 & 0 \\
\text{M-E} & 1-c & 0 & 0 & c & 0 & 0 \\
\text{F} & 0 & S_t*(1-f)*(1-c) & (1-S_t)*(1-c) & S_t*f & S_t*(1-f)*c & (1-S_t)*c \\
\text{A-R} & 0 & S_t*(1-f)*(1-c) & (1-S_t)*(1-c) & S_t*f & S_t*(1-f)*c & (1-S_t)*c \\
\text{M-R} & 0 & S_t*(1-f)*(1-c) & (1-S_t)*(1-c) & S_t*f & S_t*(1-f)*c & (1-S_t)*c
\end{array}
$$

Figure S4. State transition matrix of the 1986-2020 multievent model for the estimation of breeder recapture probabilities. Rows indicate the states of individual spots in breeding territories i at time t, columns indicate states at time t+1. State codes are as following: E (Already empty spot), A-E (Abandonment resulting in Empty spot), M-E (Mortality resulting in Empty spot), F (Spot already occupied, no replacement), A-R (Abandonment, Replaced by new individual), and M-R (Mortality, Replaced by new individual). Parameters are c (probability of colonization), f (probability of fidelity), and S (survival probability). Subindex t indicates time (year).

$$
\begin{array}{c|ccccccccc}
t / t & \text{E} & \text{A-E} & \text{M-E} & \text{U-E} & \text{F} & \text{A-R} & \text{M-R} & \text{U-R} & \text{NS} \\
\hline
\text{E} & p_t & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_t \\
\text{A-E} & 0 & p_t*r_A & 0 & p_t*(1-r_A) & 0 & 0 & 0 & 0 & 1-p_t \\
\text{M-E} & 0 & 0 & p_t*r_M & p_t*(1-r_M) & 0 & 0 & 0 & 0 & 1-p_t \\
\text{F} & 0 & 0 & 0 & 0 & p_t & 0 & 0 & 0 & 1-p_t \\
\text{A-R} & 0 & 0 & 0 & 0 & p_t*NOR_{i,t} & p_t*(1-NOR_{i,t})*r_A & 0 & p_t*(1-NOR_{i,t})*(1-r_A) & 1-p_t \\
\text{M-R} & 0 & 0 & 0 & 0 & p_t*NOR_{i,t} & 0 & p_t*(1-NOR_{i,t})*r_M & p_t*(1-NOR_{i,t})*(1-r_M) & 1-p_t
\end{array}
$$

Figure S5. Event matrix (and initial evento matrix) of the 1986-2020 multievent model for the estimation of breeder recapture probabilities. Rows indicate the states of individual spots in breeding territories i at time t, columns indicate events at time t. State codes are as following: E (Already empty spot), A-E (Abandonment resulting in Empty spot), M-E (Mortality resulting in Empty spot), F (Spot already occupied, no replacement), A-R (Abandonment, Replaced by new individual), and M-R (Mortality, Replaced by new individual). Events indicate the probabilities of observing each state previously described, along with three more codes: U-E (individual disappearance of Unknown reason resulting in Empty spot), U-R (individual disappearance of Unknown reason, Replaced by new individual), and NS (not seen). Parameters are p (resighting probability), r_A (probability of assigning an individual disappearance of unknown reason as an abandonment), r_M (probability of assigning a disappearance as a mortality), and NOR (probability of a non-observable replacement). Subindices stand for time (t), and individual (i).

Supplementary Material S2 – Simulation of data and evaluation of potential survival biases from the French population due to permanent emigration

Because no mark-recapture schemes were active in the study population between 2000 and 2007, we could neither estimate non-breeder survival nor recruitment to the breeding population or permanent emigration probabilities. Hence, we used estimates from the neighbouring population in France for the same period of time (Hernández-Matías et al., 2011). Nevertheless, demographic parameter estimation in that study was done using a conventional multistate mark-recapture design, which generated estimates of apparent survival not separated from permanent emigration. Hence, we may be at risk of using estimates of apparent survival biased by permanent emigration for this period while using true survival in the other two periods. To avoid these issues, we performed simulations to assess the magnitude of the differences between true and apparent survival in the estimates of Hernández-Matías et al. (2011). First, we simulated encounter histories based on the demographic parameters reported in the study. Second, we analysed these simulated data under 1) a conventional multistate CMR model to obtain apparent survival estimates, and 2) a SECR model using natal dispersal data for the same population provided at Hernández-Matías et al. (2010) to estimate true survival. We described the approach and results of our simulations hereby.

Simulation of encounter histories

Based on the survival, recruitment, recapture, recovery, and tag loss estimates reported at Hernández-Matías et al. (2011), we simulated capture-recapture histories with the same number of ringed (N=423) and recruited (N=44) individuals. We analysed the data using the same state transition and observation matrices. State matrices accounted for a total of seven different states describing if individuals 1) were alive or dead, 2) retained or had lost their alphanumeric darvic rings, and 3) were either non-breeders or breeders. Seven possible observations were described in the observation matrices, which corresponded to the probability to see live individuals in any of the states or recover dead individuals. Further information can be found at Hernández-Matías et al. (2011), section *Methods:*

Model parameterization. Importantly, given the relatively low number of simulated individuals (i.e., 423), data simulation may lead to considerable variation between real and simulated datasets. Hence, we simulated and analysed 100 different datasets and by inspection of the results, we selected the one whose estimates were closer to the published results. The results of the simulation showed very similar estimates and uncertainties for most published estimates, especially apparent survival (Figure S6, Table S1).

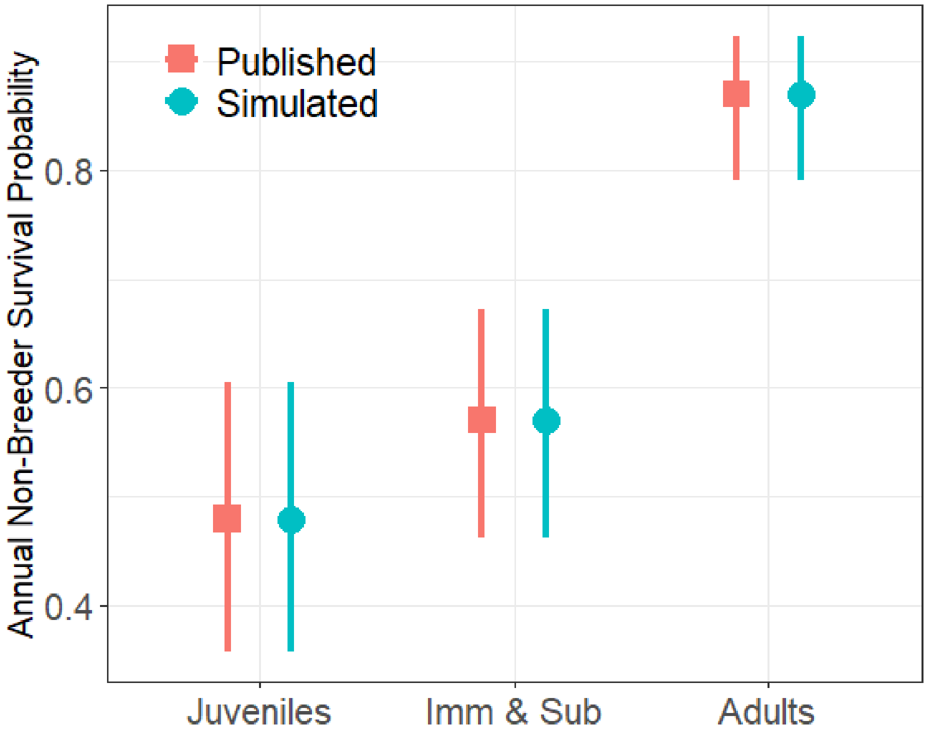

Figure S6. Estimates of apparent non-breeder survival published at Hernández-Matías et al. (2011) compared to the results of this study based on the simulated mark-resighting dataset. Estimates are provided by age class. Points indicate posterior means and error bars indicate 90% credible intervals.

Table S1. Estimates of demographic parameters published at Hernández-Matías et al. (2011) compared to the results of the simulations conducted in this study. Values are provided with means and 95% confidence intervals for published estimates (i.e., from frequentist analysis), and with posterior means and 95% credible intervals for simulated data. Abbreviation "yo." stands for "years old".

	Published	**Simulated**
Parameter	Mean ± 95%CI	Mean ± 95%CRI
Recruitment (1 yo.)	0.017 (0 – 0.041)	0.007 (0 – 0.028)
Recruitment (2 yo.)	0.176 (0.064 – 0.288)	0.101 (0.041 – 0.185)
Recruitment (3 yo.)	0.605 (0.347 – 0.862)	0.522 (0.357 – 0.689)
Recruitment (4 yo.)	0.105 (0 – 0.217)	0.156 (0.031 – 0.404)
Resighting (NB)	0.040 (0.026-0.063)	0.044 (0.029 – 0.063)
Resighting (B)	0.614 (0.505 – 0.713)	0.592 (0.519 – 0.664)
Six-month tag loss	0.059 (0.038 – 0.092)	0.054 (0.039 – 0.071)
Recovery	0.109 (0.080 – 0.143)	0.120 (0.090 – 0.153)

Comparison of apparent and true survival using conventional and spatially-explicit mark-recapture models

To evaluate potential differences between the apparent survival estimates provided at Hernández-Matías et al. (2011) and estimates of true survival, we analysed the simulated mark-recapture dataset using the spatially-explicit capture-mark-recapture formulation (SECR) from Badia-Boher et al. (2023). To tear apart true survival from permanent emigration, this formulation requires a joint analysis of survival and natal dispersal data. Thus, we used natal dispersal data from the same marked population and period of Hernández-Matías et al. (2011) (i.e., areas of birth and natal dispersal distances, n = 44 individuals), which were reported at Hernández-Matías et al. (2010). We assigned those birth areas and corresponding natal dispersal distances to each of the 44 recruited individuals in the simulated mark-recapture dataset. In the SECR model, the state transition matrix incorporated the joint estimation parameter P_d, which explicitly models the permanent emigration process (Figure S7). The observation matrix remained the same (Figure S8).

$$
\begin{array}{c|ccccccc}
t / t+1 & \text{ANB-PM} & \text{ANB-M} & \text{AB-PM} & \text{AB-M} & \text{DNB} & \text{DB} & \text{AS} \\
\hline
\text{ANB-PM} & (S_a * (1-\gamma_a) * (1-tl)) & (S_a * (1-\gamma_a) * tl) & \left(S_a * \gamma_a * P_{d_i} * (1-tl)\right) & (S_a * \gamma_a * P_{d_i} * tl) & ((1-S_a) * (1-\gamma_a) * r) & \left((1-S_a) * \gamma_a * P_{d_i} * r\right) & *_A \\
\text{ANB-M} & 0 & S_a * (1-\gamma_a) & 0 & (S_a * \gamma_a * P_{d_i}) & ((1-S_a) * (1-\gamma_a) * r) & \left((1-S_a) * \gamma_a * P_{d_i} * r\right) & *_B \\
\text{AB-PM} & 0 & 0 & S_a * (1-tl) & S_a * tl & 0 & (1-S_a) * r & (1-S_a) * (1-r) \\
\text{AB-M} & 0 & 0 & 0 & S_a & 0 & (1-S_a) * r & (1-S_a) * (1-r) \\
\text{DNB} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\text{DB} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\text{AS} & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}
$$

$$*\mathrm{A}: ((1-S_a) * (1-r)) + \left(S_a * \gamma_a * (1-P_{d_i})\right) + \left((1-S_a) * \gamma_a * (1-P_{d_i})\right)$$

$$*\mathrm{B}: ((1-S_a) * (1-r)) + \left(S_a * \gamma_a * (1-P_{d_i})\right) + \left((1-S_a) * \gamma_a * (1-P_{d_i})\right)$$

*Figure S7. State transition matrix of the 1990-2008 multistate model from Hernández-Matías et al. (2011) adapted to the spatially-explicit framework. Rows indicate the states of individuals i at time t, columns indicate states at time t+1. The matrix includes the parameters S (survival), γ (recruitment to the breeding population), Pd (joint-estimation parameter), tl (PVC ring loss probability), and r (probability of encountering a dead marked individual). Subindices indicate age (a), and individual (i). States are Alive as Non-Breeder with PVC and Metal rings (ANB-PM), Alive as Non-Breeder with Metal ring only (ANB-M), Alive as Breeder with PVC and Metal rings (AB-PM), Alive as Breeder with Metal ring only (AB-M), Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Due to the length of the first and second absorbing state expressions (i.e., transition from ANB states in t to AS in t+1), we wrote these expressions outside the matrix (*A,*B).*

$$
\begin{array}{c|ccccccc}
t / t & 1 & 2 & 3 & 4 & 5 & 6 & 7 \\
\hline
\text{ANB-PM} & p_{NB} & 0 & 0 & 0 & 0 & 0 & 1-p_{NB} \\
\text{ANB-M} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\text{AB-PM} & 0 & 0 & p_B & 0 & 0 & 0 & 1-\mathrm{p_B} \\
\text{AB-M} & 0 & 0 & 0 & p_B & 0 & 0 & 1-\mathrm{p_B} \\
\text{DNB} & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
\text{DB} & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
\text{AS} & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}
$$

Figure S8. Observation matrix for the French population from Hernández-Matías et al. (2011) adapted to the spatially-explicit formulation to estimate true survival. Rows indicate the states of the individual i at time t, columns indicate observations/events of individuals i at time t. The matrix includes the parameters p_{NB} (non-breeder recapture) and p_B (breeder recapture). States are Alive as Non-Breeder with PVC and metal rings (ANB-PM), Alive as Non-Breeder with metal ring only (ANB-M), Alive as Breeder with PVC and metal rings (AB-PM), Alive as Breeder with metal ring (AB-M), Dead as Non-Breeder (DNB), Dead as Breeder (DB), and Absorbing State (AS). Observations/Events 1 to 7 have equivalent meanings to the states except for code 7 (Not Seen).

Our results showed no differences between apparent and true survival (i.e., <0.5 on average, Figure S9). These findings suggest that the estimates provided at Hernández-Matías et al., (2011) were not affected by permanent emigration.

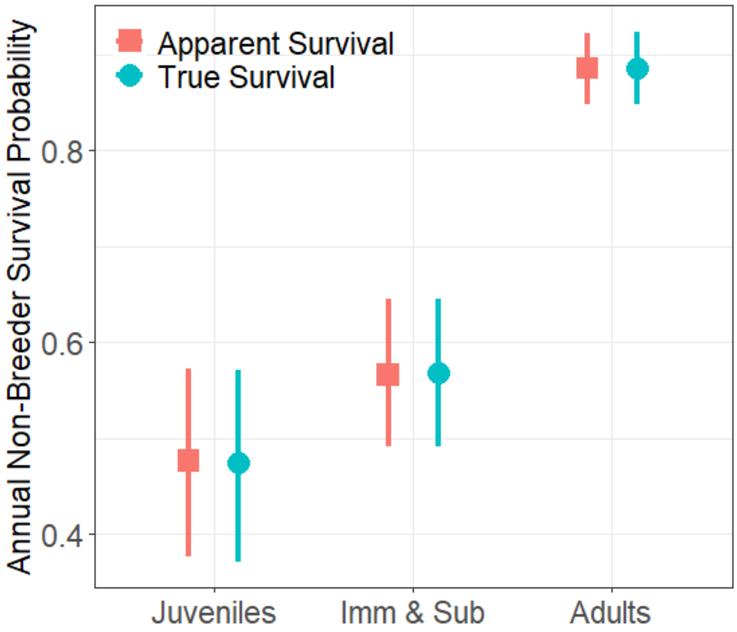

Figure S9. Comparison between the estimates of apparent and true survival from the analyses of simulated mark-recapture datasets. Estimates are provided by age class. Points indicate posterior means and error bars indicate 90% credible intervals.

These findings may be explained because natal dispersal in the French population was reported as considerably lower than that found in Catalonia (Hernández-Matías et al., 2010). In fact, our estimate of permanent emigration for the French population was 11.5%, (90%CRI = 6.3% - 15.8%), which is considerably lower than the range of values reported for the Catalan population (30-45%, Badia-Boher et al., 2023 and this study). In addition, Hernández-Matías et al. (2011) incorporated resightings and recoveries both from France and neighbouring Catalonia. Because the French population is at the northern apex of the range of the species in western Europe and is contiguous to the Catalan population to the south, most individuals that permanently leave the study area likely recruit in the Catalan population. These particularities may result in mark-reencounter schemes detecting the vast majority of recruited individual, leading to the estimation of true survival without the need for spatially-explicit models. Therefore, based on our findings, the estimates of non-breeder survival and recruitment from Hernández-Matías et al. (2011) were appropriate to be used for the 2000-2007 period in our study.

References

Hernández-Matías, A., Real, J., Pradel, R., Ravayrol, A., & Vincent-Martin, N. (2011). Effects of age, territoriality and breeding on survival of Bonelli's Eagle Aquila fasciata. Ibis, 153(4), 846–857.

Badia-Boher, J. A., Real, J., Riera, J. L., Bartumeus, F., Parés, F., Bas, J. M., & Hernández-Matías, A. (2023). Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark-recapture analyses. *Scientific Reports*, 13(1), 6970.

Supplementary Material S3 – Report of the rest of parameters estimated in multievent and spatially-explicit multistate models

Table S2. Posterior means and 90% credible intervals of the rest of parameters estimated in the 1986-1999 spatially-explicit capture-mark-recapture model (SECR).

SECR model 1986-1999

Parameter	Mean ± 90%CRI
Non-breeder resighting	0.060 (0.031 – 0.086)
Breeder resighting	0.604 (0.425 – 0.788)
Recovery	0.269 (0.195– 0.344)
Metal ring loss	0.041 (0.002 – 0.078)
PVC ring loss	0.240 (0.156-0.325)

Table S3. Posterior means and 90% credible intervals of the rest of parameters estimated in the 2008-2020 spatially-explicit capture-mark-recapture model (SECR).

SECR model 2008-2020

Parameter	Mean ± 90%CRI
Non-breeder resighting	0.048 (0.037 – 0.058)
Breeder resighting	0.85 (0.65-0.98)
Non-breeder recovery	0.237 (0.189 – 0.284)
Breeder recovery	0.263 (0.151 – 0.375)

Table S4. Posterior means and 90% credible intervals of the rest of parameters estimated in the 1986-2020 multievent capture-mark-recapture model for the estimation of breeder survival from territory replacements.

Multievent model 1986-2020

Parameter	Mean ± 90%CRI
Empty spot colonization	0.346 (0.321 – 0.371)
Spot fidelity	0.965 (0.946-0.987)
NOR (Grand mean)	0.344 (0.230 – 0.490)
Assignment of mortality	0.358 (0.180 – 0.318)
Assignment of abandonment	0.358 (0.132 – 0.604)
Observation (Grand mean)	0.876 (0.781 – 0.972)

CHAPTER 4

Assumptions about survival estimates and dispersal processes can have severe impacts on population viability assessments

Photograph courtesy of Jaume Elies

Badia-Boher, J. A., Real, J., & Hernández-Matías, A. (2023). Assumptions about survival estimates and dispersal processes can have severe impacts on population viability assessments. *In preparation for submission (Biological Conservation)*.

Assumptions about survival estimates and dispersal processes can have severe impacts on population viability assessments

Author 1: Jaume A. Badia-Boher[1*]

Author 2: Joan Real[1]

Author 3: Antonio Hernández-Matías[1]

[1]Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia I Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Spain.

Abstract

Population viability analysis (PVA) is a central tool for conservation decision-making. To ensure the reliability of PVA projections, it is important to identify factors that can introduce inaccuracies or biases. This study addresses two general but frequently overlooked related issues in PVAs that can significantly affect the reliability of their projections. First, we examined the effects of using apparent survival versus true survival estimates on PVA outcomes. Second, we incorporated emigration and immigration into the models to assess their influence on the accuracy of projections based on each type of survival estimate. To evaluate these concerns, we implemented individual-based demographic PVAs structured by age, sex, and breeding status using a Bonelli's eagle population in Catalonia as a study system, from which apparent and true survival estimates were available (2008-2020). The performances of PVA projections based on each type of survival estimate and migration process were assessed by evaluating their fit to census data. Our findings revealed that projections based on apparent survival resulted in a population decline, whereas those based on true survival predicted an increase and fitted observed data significantly better. However, true survival may only project population dynamics accurately if emigration and immigration are at balance. Conversely, using apparent survival may systematically underestimate population dynamics if immigration is not modelled. Because information on migration processes is rarely available, calibrating projections against observed data may be fundamental to test the adequacy of survival estimates. Alternatively, recently developed analytical methods may permit an easier estimation of migration processes.

Introduction

Population viability analysis (PVA) - the use of quantitative methods to model the future trends of wild populations – is a central tool in conservation science and practice (Brook et al., 2000; Himes Boor, 2014; Chaudhary & Oli, 2020). PVA results have become the pillars of conservation assessments and decision-making, as they are regarded as an objective methodology that provides management criteria based on biological and demographic arguments (Morris & Doak, 2002; Chaudhari & Oli, 2020). PVAs can be used to predict short and long-term extinction risks (Ralls et al., 2002; Folt et al., 2021), determine the most important vital rates for population growth (Morris & Doak, 2002), identify the causes of population declines (Perlut et al., 2008), design measures to control invasive species (Berg, 2012), evaluate the potential effects of future threats (Lunney et al., 2007), compare potential management scenarios and pinpoint those that ensure population persistence (Bakker et al., 2009; Hostettler et al., 2013; Badia-Boher et al., 2022), understand the spatial dynamics of populations and metapopulations (Hernández-Matías et al., 2013; Fryxell et al., 2020), establish population harvest limits (Bradshaw et al., 2013), and manage wildlife diseases (Frick et al., 2010).

Given the central role of PVAs in conservation decision-making, it is essential that PVAs deliver unbiased results that accurately describe or predict the dynamics of populations. Nevertheless, several concerns have been raised about the reliability of PVA predictions (Beissinger & Westphal, 1998; Coulson et al., 2001; Reed et al., 2002; Chaudhary & Oli, 2020). First, if there is a lack of precise knowledge about the life cycle of the study species, PVAs may not accurately represent relevant demographic processes and population stages, leading to potentially poor PVA structure and unreliable results (Doak et al., 2002). Second, poor-quality demographic data may lead to imprecise demographic estimates, which may result in too uncertain PVA outcomes that may be useless for conservation decision-making (Beissinger & Westphal, 1998; Ralls et al., 2002). Third, an inadequate modelling of uncertainty and stochastic population processes may lead to biases and/or overconfidence in PVA outcomes (Morris & Doak, 2002; Henle et al., 2004 McGowan et al., 2011). Importantly, imprecise, overconfident, or biased PVA results may lead to wrong or uninformative assessments of the conservation status and prospects of wild populations, and consequently, inadequate management decisions (Beissinger and

Westphal, 1998; Chaudhary & Oli, 2020). Hence, identifying and addressing potential constraints and limitations of PVAs constitutes a major priority to increase the global effectiveness of conservation action.

Demographic PVAs (also known as stage-structured models) are the most used type of PVAs at present (Chaudhary & Oli, 2020). In contrast to simpler, count-based models, demographic PVAs enable an accurate representation of the life cycle of the species by means of including age and stage structures in vital rates. Importantly, these PVAs usually focus on the modelling of birth and mortality processes using fecundity and survival estimates respectively, while most designs do not explicitly account for emigration and immigration processes (Morris & Doak, 2002). This approach is frequently taken for convenience as information about dispersal processes is rarely available (Williams et al., 2002; Millon et al., 2019). However, wild populations closed to migratory fluxes are the exception rather than the norm (Hanski, 1999; Matthysen et al., 2012). In fact, immigration and emigration can have a considerable influence in population dynamics, and therefore ignoring these processes in population models might lead to poor predictions of population viability (Schaub et al., 2010; Mihoub et al., 2011; Altwegg et al., 2014; Harman et al., 2020). PVA structures that incorporate emigration and immigration processes exist and are known as metapopulation PVAs or spatially-explicit PVAs (e.g., Harrison et al. 2011; Hernández-Matías et al., 2013, Fryxell et al., 2020). However, these models are especially data-hungry and are more complex to implement, and thus their applicability is limited to extensively studied species and generally discarded for threatened species with lower population sizes, which are the most common targets of PVAs.

Survival is frequently the parameter with the largest influence on population growth rates (Saether & Bakke, 2000). Hence, robust estimates of survival are fundamental to obtain reliable PVA projections. In demographic PVAs, stage-structured survival estimates are often obtained from capture-mark-recapture analyses (CMR, e.g., Bakker et al., 2009; Taylor et al., 2009; Bradshaw et al., 2013). Importantly, CMR analyses provide two types of survival estimates: true and apparent survival. True survival (S) is a neat probability of survival. Instead, apparent survival (φ) is the product of true survival and site fidelity (White & Burnham, 1999). Hence, in populations where permanent emigration from the study area exists (i.e., site fidelity is lower than 1), apparent survival may be lower than true survival (Marshall et al., 2004; Schaub & Royle, 2014; Badia-Boher et al., 2023). Apparent survival is more widely reported, first, as most study areas are subject to permanent emigration, and second, because the most extended CMR formulations cannot distinguish between both mortality and permanent emigration (Lebreton et al., 1992; White & Burnham, 1999). Nevertheless, recent developments in CMR analysis are providing more accessible formulations to estimate true survival in a wider range of scenarios (Gilroy et al., 2012; Schaub & Royle, 2014; Badia-Boher et al., 2023). Given the sensitivity of population growth rates to survival, it appears likely that the differences between apparent and true survival could lead to considerably different population forecasts in the same population. This apparently important point has received considerably low attention in the PVA literature, especially when compared to other issues in these models. For example, popular evaluations and reviews of the factors that affect the reliability and the accuracy of PVAs do not mention this topic (i.e., Beissinger & Westphal, 1998, Brook et al., 2000; Reed et al., 2002; Chaudhary & Oli, 2020). Additionally, the effects of the type of survival used on PVAs may be wider (Figure 1). If apparent survival is used, emigration processes are accounted for implicitly. In these cases, if immigration is not considered, this may constitute a disbalance in which all population processes that lead to individual loss are modelled (i.e., death and emigration), but individual-gaining processes are only modelled partially (i.e., birth). Hence, the use of apparent survival in demographic PVAs could lead to a considerable risk of underestimating population viability except in cases where immigration is not present or residual. On the other hand, if true survival is used, emigration is not accounted for implicitly. Intuitively, the use of true survival may be more adequate in populations where emigration and immigration cancel each other out (i.e., Emigration – Immigration = 0), so that population dynamics basically depend on birth and death processes. In any other situations, this parameter could also lead to imbalances between the true and the modelled dynamics.

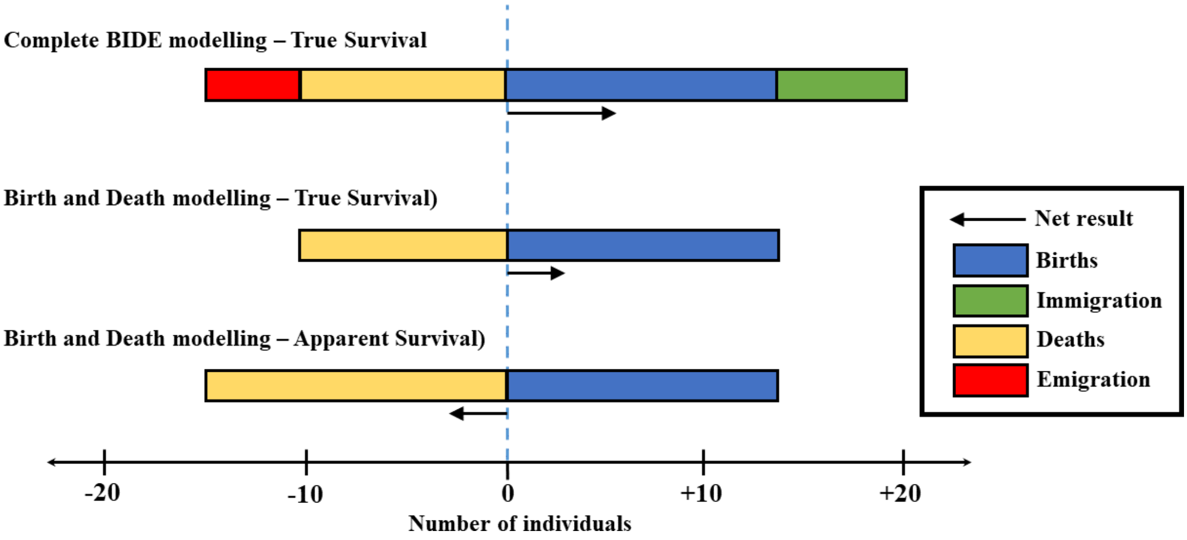

Figure 1. Example of the potential effect of the type of survival use on the modelling of population dynamics in Population Viability Analysis. This case reflects a population where immigration slightly exceeds emigration and births exceed deaths. The complete modelling of all four BIDE processes (i.e., Birth, Immigration, Death, Emigration) would predict a population increase. The use of true survival without any explicit modelling of migration processes could lead to an underestimation of population growth. Instead, if apparent survival was used, emigration would be accounted for implicitly but not immigration, which could result in projections of population decline.

The high popularity of demographic PVAs, the large availability of user-friendly software, and the traditional lack of information about dispersal processes has favoured a sustained use of these models for decades, which may probably continue in future years (Brook et al., 1999; Chaudhary & Oli, 2020). Hence, it is urgent to 1) quantify how the use of either apparent or true survival may lead to different predictions of population viability, and 2) understand how the explicit modelling of migration processes may modify the reliability of predictions based on either of both estimates. In this study, we aim at gaining insights about these topics using as a basis an extensively studied, regionally threatened raptor population, the long-lived Bonelli's eagle in Catalonia. The life cycle of this species is known in detail thanks to the extensive literature available, which favours a precise PVA design (Real & Mañosa, 1996, 2001; Cadahía et al., 2010; Hernández-Matías et al., 2010, 2011, 2013). In addition, population estimates structured by sex, age, and breeding status are available for both apparent and true survival thanks to recent analyses based on spatially explicit CMR models (2008-2020; Badia-Boher et al., 2023). Based on these data, we first built individual-based demographic PVAs without an explicit modelling of migration processes and representing the relevant processes in the life cycle of the species (i.e., mortality, birth, recruitment to the breeding population, mating, and reproduction) in a population structured by age, sex, and breeding status. We evaluated the fit of these PVAs using true and apparent survival estimates to the observed population numbers between 2008 and 2020. This way, we could assess the ability of either model to retrieve the true dynamics of the population. Second, we projected the models 30 years into the future to compare the predicted trends under each survival type. Third, we built PVAs with similar structures but including different numbers of 1) emigrants and immigrants when using true survival, and 2) immigrants when using apparent survival. We evaluated the fit of their outcomes to the observed population numbers between 2008 and 2020 to assess how immigration and emigration processes may affect PVA predictions and accuracy. Finally, we discussed aspects to consider when using different survival estimates in demographic PVAs and analytical solutions to improve their reliability when modelling populations where migration processes exist.

Methods

Study population and life cycle

The Bonelli's eagle (*Aquila fasciata*) is a long-lived territorial raptor whose range extends from southeastern Asia through the Middle East to the western Mediterranean. In continental western Europe, the total breeding population has been estimated at 920 to 1100 pairs, of which ca. 80% are located in the Iberian Peninsula (del Moral & Molina, 2018; BirdLife International, 2019). Here, we focus on the local population in Catalonia, located at the north-east of Spain. The species distribution in Catalonia ranges from the French border in the north to the southern limits of the Ebre Delta and is characterized by Mediterranean landscapes and habitats between 0 and 800 m asl. As most populations in western Europe, the study population underwent a considerable decline in the second half of the 20th century, from ca. 85-90 breeding pairs in the 1970s to ca. 63 pairs in 2000, followed by a recovery to ca. 82 territories in 2020 (del Moral & Molina, 2018). The Catalan population has been intensively monitored for decades (Real & Mañosa, 1996, 2001; Hernández-Matías et al., 2015; Badia-Boher et al., 2023). An intensive tag-resighting scheme was launched between 2008 and 2020, in which 461 chicks were ringed in their nests with both alphanumeric and metal rings. Of these, 105 were recontacted and

83 were seen recruited as breeders, and 78 were found dead. In addition, breeding territories were monitored during the breeding season (yearly mean: 55) to assess the number of fledglings raised by breeding pair and year.

As a long-lived species, the Bonelli's eagle shows a relatively large life expectancy, delayed sexual maturity, and low reproductive rates (Hernández-Matías et al., 2010, 2013). Like other territorial raptors, Bonelli's eagle populations are structured between territorial (i.e., breeders), and non-territorials individuals (non-breeders). Both population stages show considerable differences in their behavioural patterns and space uses. After the post-fledgling dependence period and before individuals recruit to breeding territories, Bonelli's eagles pass through a transient nomadic phase typically known as the dispersal period (Real & Mañosa, 1996). At this life stage, individuals can disperse long distances up to hundreds of kilometers away from their territories of birth to reach areas with large prey availability and prospect potential breeding areas (Real & Mañosa, 2001; Cadahía et al., 2010). Individuals recruit to breeding territories at a varying age, but mostly between 3 and 4 years (Hernández-Matías et al., 2010). Once recruited, individuals show strong pair-bonding behaviour with strong fidelity to their breeding areas throughout the year and throughout their lives (Bosch et al., 2010; Hernández-Matías et al., 2011).

Apparent and true survival estimation

We used the estimates of apparent and true survival structured by age, sex, and breeding status in the Catalan Bonelli's eagle population from Badia-Boher et al. (2023). For non-breeders, survival was estimated differently for juveniles (1 year old), immatures plus subadults (2-3 years old), and adults (4 years old and older; Hernández-Matías et al., 2011). For breeders, it was estimated as constant for all ages, which is reasonable considering the reported behavioural once birds recruit into breeding territories (Hernández-Matías et al., 2011). All estimates were obtained separately for males and females. Apparent survival was estimated using a conventional multistate model. Instead, true survival was estimated using a Bayesian spatially-explicit CMR formulation, which permits the separation of true survival and permanent emigration probabilities (see Badia-Boher et al. 2023 for details). We modelled the results obtained under lognormal natal dispersal kernel distributions. Results showed considerable differences in the apparent and true survival estimates of non-breeders (Table 1). This was expectable as non-breeders show very large dispersal patterns compared to breeders, and hence may be more likely to emigrate from the study area. Instead, apparent and true breeder survival were practically identical. Additionally, differences between apparent and true non-breeder survival were larger for females. The reason for these differences was that like in most bird species, Bonelli's eagle females show larger dispersal patterns than males, which can result in larger permanent emigration probabilities, and subsequently, a larger effect on apparent survival estimates (Pusey et al., 1987; Schaub & Royle, 2014).

Table 1. Apparent and true survival estimates of the Bonelli's eagle population in Catalonia (2008-2020) structured by breeding status, age class, and sex (published at Badia-Boher et al., 2023). Abbreviation yo. stands for "years old". Estimates are reported as posterior means and 90% credible intervals.

Estimate	Age	Sex	Apparent Survival	True Survival
Non-breeder survival	1 yo.	Female	0.627 (0.533 - 0.731)	0.674 (0.580 - 0.764)
		Male	0.611 (0.509 - 0.711)	0.648 (0.555 - 0.742)
	2-3 yo.	Female	0.626 (0.524 - 0.722)	0.701 (0.613 - 0.785)
		Male	0.739 (0.645 - 0.828)	0.758 (0.666 - 0.841)
	Adults	Female	0.818 (0.642 - 0.976)	0.892 (0.775 - 0.991)
		Male	0.839 (0.719 - 0.942)	0.848 (0.727 - 0.954)
Breeder survival	(all)	Female	0.877 (0.805 - 0.944)	0.872 (0.800 - 0.940)
		Male	0.886 (0.834 - 0.932)	0.890 (0.845 - 0.937)

Fecundity estimation

To model reproduction and birth processes, we estimated fecundity as the number of fledged chicks per breeding pair (also known as productivity). Our data were obtained from long-term reproduction surveys in our study population, in which a subset of the total breeding population was monitored for the whole breeding season during the study period (i.e., 2008-2020). We modelled productivity as a Poisson process (Kéry & Schaub, 2012):

$$J_t = Poisson(R_t * prod_t)$$

in which the number of fledged chicks J was the product of the number of monitored breeding pairs R and our productivity estimate $prod$. For this calculation, we used a Bayesian hierarchical modelling approach using r package JAGS (Plummer, 2017). We ran models in 4 chains for 160000 iterations of which we discarded the first 110000.

Demographic population viability analysis

We built an individual-based model based on a post-breeding census. The model represented life-cycle processes stepwise in one-year steps in this order: 1) survival / mortality, 2) aging, 3) recruitment to the breeding population, 4) breeding territory acquisition (the number and identity of breeding territories are explicitly accounted in the model), 5) mating, and 6) breeding. We considered parametric uncertainty in all estimates. For productivity, we decomposed parametric uncertainty into sampling and temporal variance following Morris & Doak (2002) and incorporated both uncertainty estimates sequentially into the model following McGowan et al. (2011). Since survival estimates were time-constant, we could not decompose variances into sampling and temporal variance (White, 2002; McGowan et al., 2011). Hence, for a more honest propagation of uncertainty, we implemented parametric uncertainty at the beginning of each simulated year as a random draw from each estimate's posterior samples obtained at Badia-Boher et al. (2023). We considered demographic stochasticity when modelling mortality (Morris & Doak, 2002). Senescence was incorporated by reducing survival probabilities to 50% in individuals aged 20 years and older (Chantepie et al., 2016). We modelled recruitment to the breeding population as the permanent acquisition of a territory by a non-breeding eagle, following the biology of the species. After mortality, a number of vacant male and female spots in breeding territories became available. The model prioritizes the occupation of these vacant spots in occupied territories instead of the occupation of new territories, following the observed behaviour of this and other territorial raptors (Hernández-Matías et al., 2010). We allocated live non-breeders to territories giving priority to older ages to represent a competitive advantage provided by age (Penteriani et al., 2003). One-year-old individuals were not allowed to recruit, following estimates in former works showing that recruitment of juveniles was very rare (i.e., less than 1-2%

chance; Hernández-Matías et al., 2010; Badia-Boher et al., 2023). Since in raptor populations recruitment to breeding territories is often limited by more factors than just breeding spot availability (i.e., recruitment probabilities are rarely one, even in populations not limited by density dependence such as recently reintroduced populations; Badia-Boher et al. 2022), we limited the number of non-breeding adults and subadults available to recruit to 80%, and immatures to 30% following observed values (Hernández-Matías et al., 2010; Badia-Boher et al., 2022, 2023). In cases where all vacant spots in formerly occupied breeding territories were filled and a number of non-breeders were still available to recruit, we allowed individuals to form new territories. However, we limited the number of new territories formed per year to either one, two, or three chosen randomly, following observed yearly increases detected by census data in the study population. We added this limitation for biological realism, as the creation of new territories is often limited by several factors such as the respective quality of potential new and occupied territories, density-dependence processes in the breeding and the non-breeding population, and availability and compatibility between mates (Hunt, 1998; Penteriani et al., 2011). We considered density dependence by adding a ceiling of 105 breeding territories in the population, i.e., 15% more than the historical peak number of breeding territories occupied reported in long-term census data (1970-2020). Breeding was simulated assuming an equal sex ratio.

PVAs incorporating emigration and immigration

In these models, we accounted for permanent emigration (hereafter, “emigration”) and permanent immigration (hereafter, “immigration”) respectively, that is, the modelling of emigrants that will never return to the local population, and immigrants that will never leave it once arrived. In Bonelli’s eagles, as in other territorial raptors, emigration and immigration occur at the time of natal dispersal, as individuals usually show strong fidelity to their first territories of recruitment, and breeding dispersal is rare and restricted to short distances (Bosch et al., 2010; Badia-Boher et al., 2023). Hence, we modelled emigration as the removal of individuals available to recruit to a breeding territory, and immigration was modelled as the addition of new individuals as potential recruits. The sex of the leaving or newcome individuals was modelled assuming an equal sex ratio. We simulated emigration and immigration of one, three, five, seven, and nine individuals when using true survival. Instead, for apparent survival scenarios, we only modelled immigration, as apparent survival already accounts for permanent emigration implicitly.

Model settings and evaluation of results

We ran 1) true and apparent survival PVAs without an explicit modelling of migration processes for the period 2008-2020, 2) the same models 30 years into the future (2020-2049), and 3) true and apparent PVAs including migration processes for the period 2008-2020. The initial population size for models starting at 2008 was chosen using breeder and fledgling census data from 2008 (i.e., 68 pairs and 63 fledglings), and mean non-breeder population size numbers estimated from unpublished integrated models (i.e., 61 individuals). Using the same data sources, models starting at 2020 began with 81 breeding pairs, 80 fledglings, and 104 non-breeders. Each model was run for 10000 replicates. Models were built using R 4.3.0 and package PopBio (Stubben & Milligan, 2007).

To evaluate the fit of 2008-2020 models to the observed number of breeding pairs, we first calculated the observed population growth rate (i.e., "observed lambda", λ_o) from census data as the final divided by the initial number of observed breeding pairs. Then, we assessed each model's probability of retrieving λ_o given their set of predicted lambdas (λ_e). To do so, we calculated the absolute distances between the 50th percentiles of predicted lambdas for each PVA and the percentile of λ_o under the set of predicted lambdas (Beaumont et al., 2005; Soares d'Oliveira et al., 2016; D'Agostino & Stephens, 2017). We named this estimate *D* (i.e., "distance"). Values ranged between 0 and 0.5, where values closer to 0 indicated a better fit of model predictions to λ_o.

Productivity estimates were shown in mean posterior values and 90% credible intervals. The results of PVA projections were reported as the mean numbers of breeding pairs and corresponding 90% interpercentile ranges between 2.5 and 97.5 percentiles of all replicates (hereafter referred to as the 90% confidence interval, 90%CI).

Results

Productivity modelling and variance decomposition

Mean productivity for the period between 2008 and 2020 was estimated at 0.906 (90%CRI 0.695 – 1.112) fledglings per breeding pair, with a minimum in 2013 (0.716, 0.552 – 0.874) and a maximum in 2011 (1.020, 0.775 – 1.261). Parametric uncertainty decomposition into sampling and temporal variance provided values of 0.000317 and 0.010407 respectively.

Apparent versus true survival – No explicit modelling of migration processes - Fit to observed population numbers (2008-2020)

True survival models (*D* = 0.248) showed a comparatively better fit to the observed number of breeding pairs than apparent survival models (*D* = 0.476). On average, both types of models underestimated the real dynamics of the population, although these were permanently inside the 90% range of predicted trajectories in the true survival model (Figure 2). At the end of simulations (i.e., 2020), 31.0% of all trajectories in the true survival model predicted a number of pairs equal or larger than the observed (i.e., 81 pairs). Instead, only 3.6% trajectories predicted so in the apparent survival model. On average, the apparent survival model predicted a sustained decline. In particular, 72.5% trajectories predicted a final breeding population smaller than the initial one (i.e., 68 pairs), while 27.2% trajectories predicted so in the true survival model.

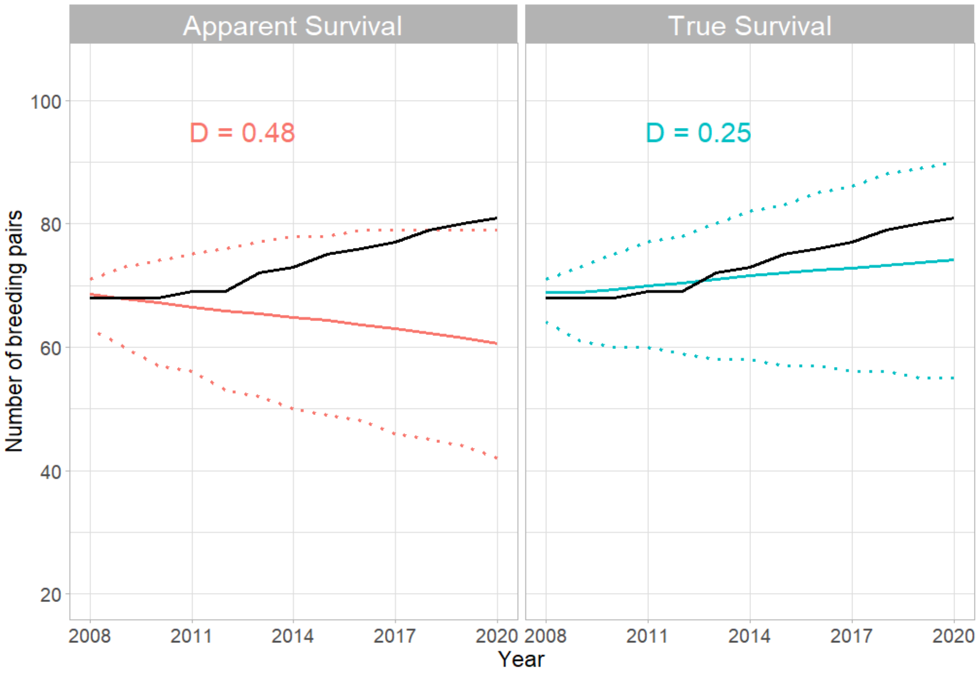

Figure 2. Means (coloured solid lines) and 90%CIs (dotted lines) of the numbers of breeding pairs projected by the PVAs between 2008 and 2020 under the use of apparent and true survival. Black lines indicate the observed numbers of breeding pairs in the study population from census data. Parameter D shows the fit of census data to PVA projections. Values closer to 0 indicate a better fit.

Apparent and true survival models – No explicit modelling of migration processes – Long-term projections (2020-2049)

The long-term projections of apparent and true survival PVAs led to opposite predictions of population growth and numbers (Figure 3). On average, the true survival PVA predicted 88 (90%CI 72-99) breeding pairs in 2030, 90 (67-105) in 2040, and 91 (63-105) in 2050. In total, 77% of all population trajectories predicted a population increase over time (i.e., final population size larger than initial, 81 breeding pairs). Only 0.17% of all trajectories predicted a decline to half the initial population size (i.e., 41 breeding pairs). Instead, the apparent survival PVA predicted on average 78 (60-93) breeding pairs in 2030, to 64 (41-88) in 2040, and 54 (30-81) in 2049. In total, 94.6% trajectories predicted a population decline over time. In addition, 21.6% trajectories declined to half the initial population size.

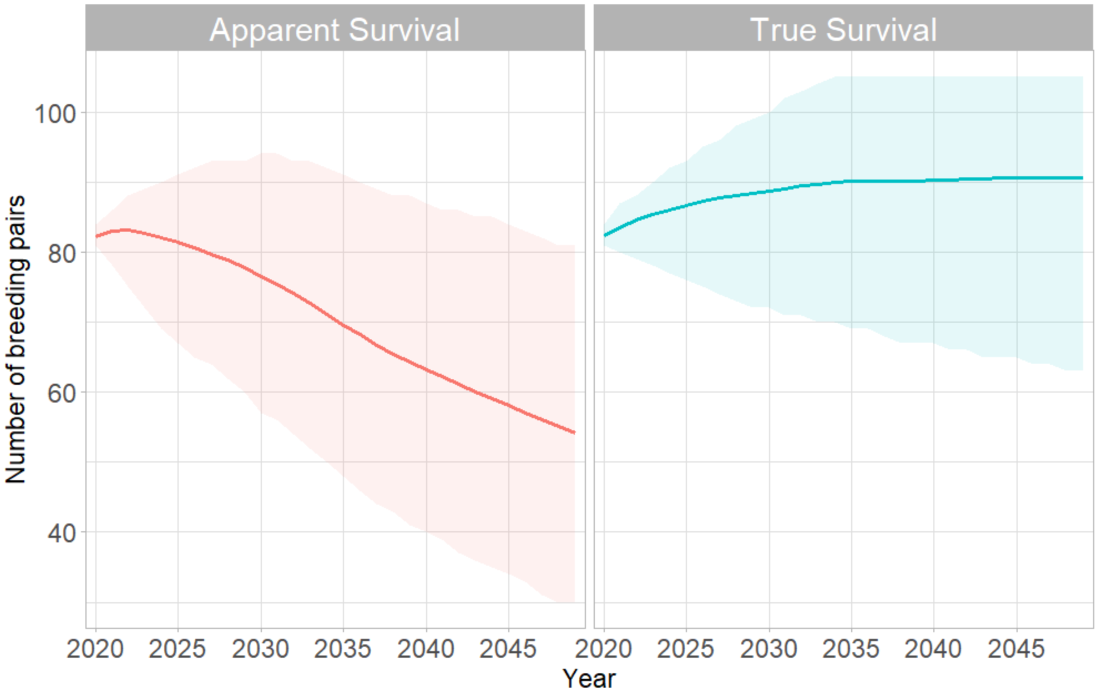

Figure 3. Means (solid lines) and 90%CIs (shaded areas) of the numbers of breeding pairs projected by the PVAs between 2020 and 2049 under the use of apparent and true survival.

<u>Explicit modelling of migration processes - Fit to observed population numbers (2008-2020)</u>

The addition of immigration in apparent survival PVAs progressively improved the fit of PVA results (Figures 4, 5). In particular, predictions reached the best fit when seven to nine immigrants were considered (*D* = 0.114 and 0.069 respectively). In true survival PVAs, progressive additions of emigrants led to worse fit and increased population declines (*D* = 0.391 for one emigrant, *D* = 0.49 for nine emigrants). Instead, the addition of small numbers of immigrants (i.e., 3) led to the best fit between the expected and the observed number of pairs (*D* = 0.061 and 0.110 respectively), while larger numbers of immigrants led to an overprediction of population growth and numbers (i.e., nine immigrants: *D* = 0.313).

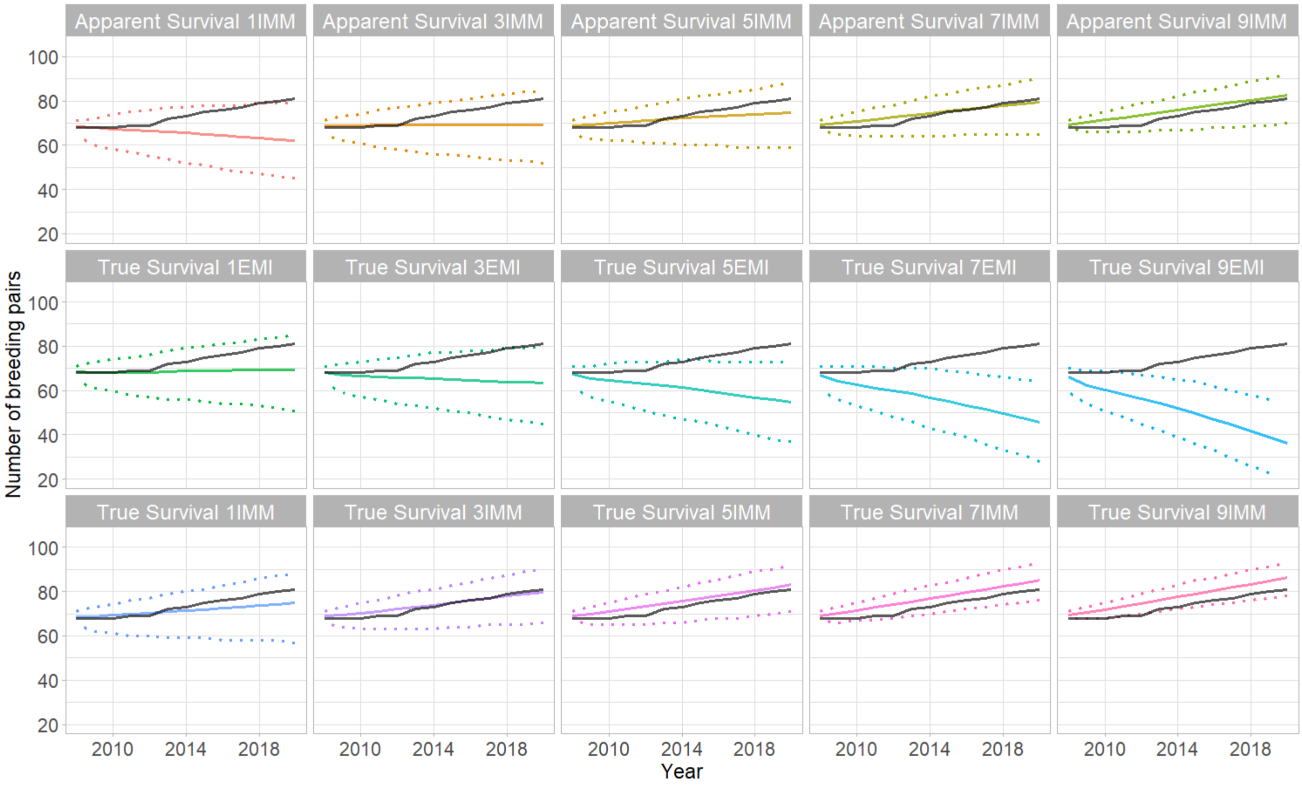

Figure 4. Means (coloured solid lines) and 90%Cis (dotted lines) of the numbers of breeding pairs projected by the PVAs between 2008 and 2020 under the use of apparent and true survival, and the explicit modelling of emigration and immigration. Black lines indicate the observed numbers of breeding pairs in the study population from census data. Subpanels are sorted as follows: row 1 shows the combination of apparent survival and 1 to 9 immigrants sequentially (left to right); row 2 shows the combination of true survival and 1 to 9 immigrants; and row 3 shows the combination of true survival and 1 to 9 immigrants.

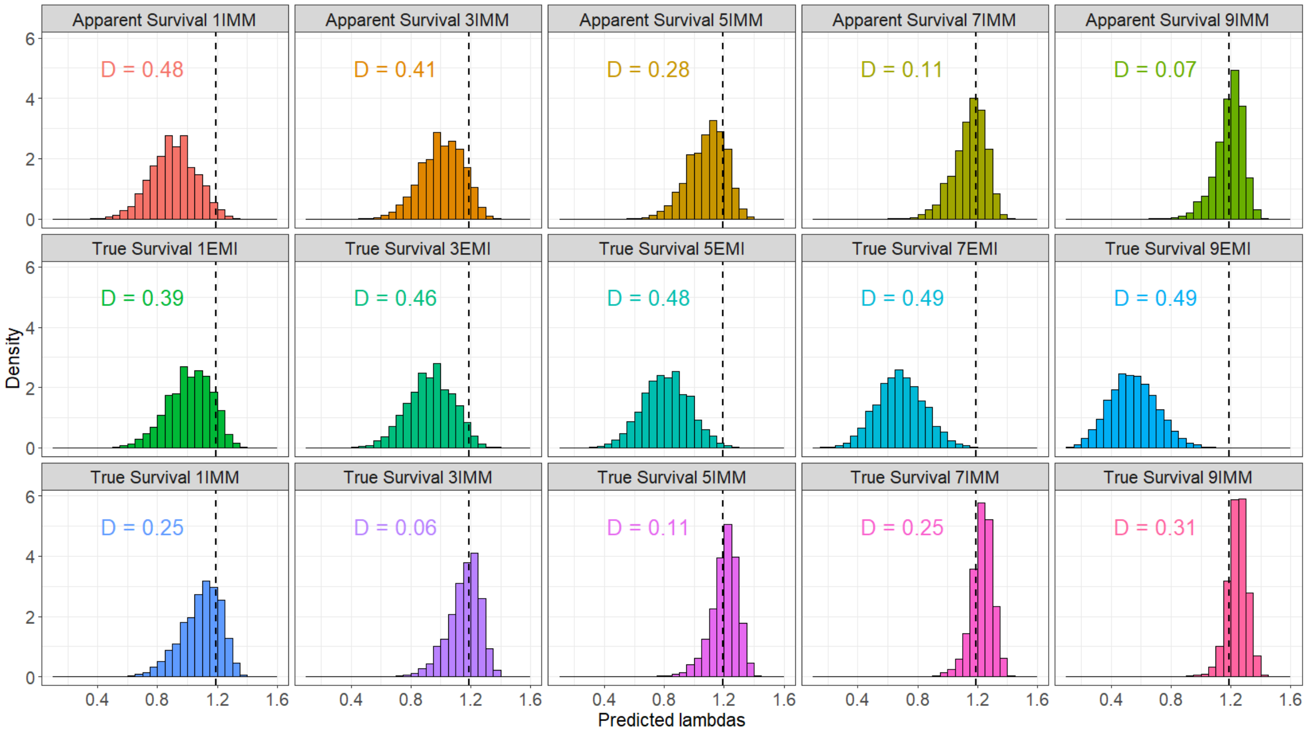

Figure 5. Histograms showing the densities of binned predicted lambdas (by groups of 0.05 units) of the PVAs projected between 2008 and 2020 under the use of apparent and true survival, and the explicit modelling of emigration and immigration. Black vertical dashed lines indicate the observed lambda from census data in the study population. Predicted and observed lambdas were calculated as the final divided by the initial number of breeding pairs. Subpanels are sorted as follows: row 1 shows the combination of apparent survival and 1 to 9 immigrants sequentially (left to right); row 2 shows the combination of true survival and 1 to 9 immigrants; and row 3 shows the combination of true survival and 1 to 9 immigrants. Parameter D shows the fit of census data to PVA projections. Values closer to 0 indicate a better fit.

Discussion

Permanent emigration is present in most wild populations and may lead to considerable differences between the estimates of apparent and true survival (Marshall et al., 2004; Schaub and Royle, 2014; Badia-Boher et al., 2023). Our results show that the use of either apparent or true survival estimates may lead to opposite predictions and considerably different fits of demographic PVAs to observed population numbers (Figures 2, 3). Additionally, the modelling of immigration may lead to improvements in the fit of models based on apparent survival, while large emigrant and immigrant numbers may lead to poorer true survival fits (Figures 4, 5). Importantly, apparent and true survival may only retrieve or predict population dynamics accurately in specific population scenarios depending on the magnitudes of emigration and immigration processes, which emphasizes the importance of either 1) calibrate model outcomes to observed data to increase confidence in future projections, or 2) accounting for migration processes explicitly in demographic PVAs. For the later, study design modifications and the use of novel analytical tools with lower data demands may favour an easier attainment of migration information and estimates (Zimmermann et al., 2007; Horton & Letcher, 2008; Abadi et al., 2011).

In our study, long-term PVA projections using apparent survival predicted a population decline, while the use of true survival led to an average increase. Interestingly, differences between the apparent and true survival estimates used in this study were concentrated in the non-breeding fraction, and were on average 0.05, 0.08, 0.08 for juvenile, subadult, and adult females respectively, and 0.03, 0.02, and 0.01 in males (Table 1; Badia-Boher et al., 2023). Since the Bonelli's eagle is a long-lived species where survival is often the largest determinant of population growth, relatively mild differences as the ones shown here may easily lead to such considerable divergence in PVA projections (Saether & Bakke, 2000). Given the large prevalence of permanent emigration, differences of this magnitude or larger between survival types may be common in wild populations. For instance, in passerine species, Schaub & Royle (2014) found increases as large as 0.2-0.3 on average in the true survival of females and 0.1-0.15 in that of males, similar to the findings of Cilimburg et al. (2002) and Paquet et al. (2020). Importantly, these types of differences may also have considerable implications for conservation and management. For instance, in our study case, the population projections of the apparent survival PVA may be sufficient to assess our study population as either Near Threatened (NT) or even threatened as Vulnerable (VU; probability of extinction > 10% in 100 years, a likely result if the duration of the PVA was extended) under the IUCN Red List Criteria (IUCN, 2012). This may justify relatively urgent management action based on the conception that the population is rapidly declining. On the other hand, models based on true survival provide high probabilities of population increase over the next 30 years (i.e., 77%), which would justify the assessment of the species as Least Concern (LC).

The 2008-2020 PVAs showed that apparent survival predicted the observed number of breeding pairs considerably worse than true survival. The reason for the poor fit of the apparent survival model may be that immigration is a relevant process in the study population, as shown by Hernández-Matías et al. (2013). When using apparent survival, PVAs fully account for population loss processes implicitly (i.e., deaths, emigration), but partially account for gain processes (i.e., only births). Hence, if immigration is present, the use of apparent survival may underestimate population numbers and viability, and consequently, overestimate extinction risks. Importantly, immigration is a frequent and sometimes central process for the dynamics of many populations (Schaub et al., 2010; Brown & Collopy, 2012; Horswill et al., 2022), and hence the risks of obtaining such biased PVA results may be considerable across populations and studies. Even so, PVA predictions based on this estimate may also be regarded as an indicator of a population's self-recruitment level, that is, its capacity to persist over time only from locally born individuals (Runge et al., 2006). This information may be of conservation interest, as population gains provided by immigration may decline if the conservation status of neighbouring populations becomes compromised. From this perspective, these "conservative" viability estimates may promote population management from a cautionary perspective. Nevertheless, researchers and managers should consider that the implementation of apparent survival in demographic PVAs across local populations and species may lead to an assignment of conservation and management priorities that may not correspond to the actual conservation needs of populations, but rather to the differential effects of emigration across them. That is, given the potential sensitivity of population growth rates to survival, large effects of permanent emigration on apparent survival may lead to more pessimistic PVA projections, while mild effects may lead to more optimistic outputs. The magnitude of permanent emigration in a study population mainly depends on two factors: 1) the dimension of the study area in respect to the species/population range (Zimmerman et a., 2007; Horton & Letcher, 2008), and 2) the dispersal capacity of the study species/population (Greenwood & Harvey, 1982; Baker et al., 1995; Newton, 1998; Chadoeuf et al., 2017). Dispersal capacities may strongly vary across different taxa, but also between different populations of the same species, or even in the same population along time (Hernández-Matías et al., 2010, 2013; Fandos et al., 2023). In addition, study area size may vary depending on the study design (Horton and Letcher, 2008). Hence, it appears essential that the interpretation of PVA outcomes based on apparent survival should include an understanding of the potential effect of permanent emigration and its main drivers.

The relatively adequate fit of the true survival PVA to observed census data may be explained because immigration and emigration were at a certain balance in the study population for the period 2008-2020, as is suggested by unpublished integrated models (own data). While this particular feature of the study population could have contributed to a better true survival fit, it should not be considered the paradigm in open populations. In fact, many populations show different scenarios where both migration processes are not at equilibrium (Schaub et al., 2010; Mihoub et al., 2011; Furrer & Passinelli, 2016). In true survival models, the modelling of small numbers of immigrants (i.e., 1 to 5) improved model fit. However, the addition of emigrants and large numbers of immigrants led to underestimations and overestimations respectively, suggesting that this type of estimate may not retrieve population dynamics accurately if migration processes exceed each another. On the other hand, the addition of immigrants progressively improved the fit of apparent survival PVAs to the observed dynamics. This finding supports our initial hypothesis predicting that apparent survival PVAs may underestimate population dynamics if immigration is not modelled.

Overall, our findings suggest that the ability of true and apparent survival to retrieve and project population dynamics accurately when migration processes are not explicitly modelled may be restricted to specific population scenarios. Thus, estimating migration processes may be critical for accurate PVA projections. In this respect, recent advances in CMR analyses and integrated models in the Bayesian framework are providing new opportunities to estimate these processes in a wide range of populations with simpler data requirements. In particular, spatially explicit models enable the estimation of emigration probabilities from the combination of mark-resighting data and the locations of sightings (Schaub & Royle, 2014; Terui, 2020; Badia-Boher et al., 2023). For example, these models estimated permanent emigration at ca. 39% in the study population (Badia-Boher et al., 2023). Another analytical tool to be considered is Integrated Population Modelling (IPMs). IPMs integrate data from multiple sources (i.e., fecundity, counts, telemetry, mark-resighting, among others) to estimate demographic parameters and population dynamics more precisely based on the shared information contained by all different sources (Schaub and Abadi, 2010). These models have the ability of estimating immigration, or even the combination of immigration and emigration, without explicit information about them based on the indirect information contained by the different data sources (i.e., as “hidden parameters”; Abadi et al., 2011). Additionally, IPMs can be easily extended into the future to perform stage-structured Bayesian Population Viability Analysis incorporating such estimates of migration processes (Schaub & Kéry, 2021). The addition of parametric uncertainty, different sources of stochasticity, and density-dependence processes is generally straightforward (Schaub & Kéry, 2021). However, individual-based designs are still under development (Petracca et al., 2023). Nevertheless, migration estimates from IPMs, and their associated uncertainties could be easily incorporated into non-Bayesian PVA structures, especially in custom-built PVAs.

Even with these improvements in the estimation of migration processes, PVAs are often used in threatened species with low population sizes and substantial data limitations, and where conservation decisions need to be made rapidly (Morris et al., 2002). In these situations, dispersal processes may be poorly or not estimable. Hence, information about the suitability of the survival estimates available may be scarce, thus compromising our ability to anticipate potential biases in PVA projections. In these cases, a potential solution may be calibrating model results to observed population numbers. As shown in this study, calibrations may inform about the ability of survival estimates to retrieve real population dynamics, which may be directly related with the effect of permanent emigration on the available estimates and the magnitudes of both migration processes in the study population. PVA calibrations have already been highlighted as a powerful tool to improve the confidence in PVA structure, life cycle, and projections (Beissinger & Westphal, 1998; Pe’er et al., 2012, Tauler et al. 2015). Following this rationale, deviations between predicted and observed population numbers in PVA calibrations may also contain information from which to extract inferences about migration processes in study populations (see Hernández-Matías et al., 2013; Tauler et al., 2014; Lieury et al., 2016). In fact, these deviations are the basis of hidden parameter estimation in IPMs to estimate migration processes (Abadi et al., 2011). Nevertheless, the degree of similarity between observed and modelled data may be a result of a variety of factors, from the accuracy of PVA structure and life cycle, to realistic representations of uncertainty, stochasticity, and density dependence (Beissinger & Westphal, 1998; Morris & Doak, 2002; McGowan et al., 2011). For example, in the case of our study, the slight underpredictions in true survival PVAs may be caused because immigration slightly exceeds emigration (own data: unpublished integrated models) but could also be caused by our approach to modelling parametric uncertainty in survival (McGowan et al., 2011). Following this example, evaluations of model calibration outputs should be performed considering all potential factors affecting the results of PVAs.

Overall, our findings suggest that understanding the contribution of migration processes to population dynamics may be essential for accurate projections of demographic PVAs. Therefore, we recommend adapting study designs and monitoring schemes where possible to obtain data for the estimation of migration processes. In this sense, potential solutions may be gathering different types of ecological data (i.e., tag-resighting, fecundity, counts) for their use in integrated analyses, and obtaining telemetry data to quantify dispersal and draw estimates on migration processes (Cadahía et al., 2010; Pfeiffer & Schaub, 2023). Alternative solutions may include enlarging study area size to diminish the effect of migration processes in local population dynamics (Zimmerman, 2007; Horton & Letcher, 2008). In situations where these solutions cannot be implemented, model calibration may be fundamental to ensure the reliability of PVA projections (Beissinger & Westphal, 1998; Pe’er et al., 2012). Additionally, we recommend discussing the potential magnitude of permanent emigration in apparent survival estimates as a critical part of the interpretation of PVA results based on these estimates, especially considering the size of the study area and the dispersal capacity of the study population. Even so, emigration, survival, and immigration dynamics may considerably vary along time together with fecundity and other key vital rates for population dynamics. However, most often, PVA projections may not have enough information to predict or account for these potential changes, especially when the information about the population/species or the sample sizes available for the estimation of demographic processes are limited. Because of this, a continuous interaction between monitoring schemes, quantitative analyses (i.e., PVAs), and conservation decision-making may be essential to maximize the benefits of PVAs as a quantitative tool for conservation (Bakker & Doak, 2009). In this respect, PVAs may serve as a framework to evaluate the effectiveness of conservation actions, and to calibrate to observed data and revisit former predictions when further demographic and ecological data become available.

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Data availability statement

The code used in this study is available in the figshare repository, https://figshare.com/s/71204a2dd24c1734c61d.

Additional information

The authors declare no competing interests.

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GENERAL DISCUSSION

Photograph courtesy of Jaume Elies

Summary of results and main findings

Population models lay at the foundation of ecological and conservation studies. Advances in the sophistication, level of detail, and flexibility of modelling methodologies in the last decades have provided the opportunity to understand population dynamics from novel and deeper perspectives and extract conclusions to guide conservation action from an evidence-based perspective. The Bonelli's eagle populations in Catalonia and Mallorca Island have been intensively monitored for years and constitute ideal study systems to generate new knowledge on the modelling, demography, and applied conservation of raptors, and more generally, long-lived animals. In this dissertation, we used data of these populations along with different modelling approaches to i) adapt novel analytical frameworks for the estimation of key demographic parameters in long-lived species, ii) gain detailed insights about the long-term dynamics of the study population and long-lived species, and 3) generate evidence-based knowledge useful for conservation decision-making. The four chapters of this thesis and their respective main findings are summarised hereby.

In **Chapter 1**, we analysed the effectiveness and cost-effectiveness of different strategies used simultaneously in the reintroduction of the Bonelli's eagle in the island of Mallorca. To do so, we developed very detailed individual-based models that enabled us to finely account for stochastic events in all main steps of the study species life cycle. Our results suggested that the relocation of non-juvenile raptors to reintroduction areas may be a cost-effective strategy to establish viable reintroduced populations. In addition, in certain scenarios this strategy may deliver better results than widely implemented methods based on the release of captive-bred fledglings. Our findings also emphasized the importance of accounting for recruitment processes in raptor reintroductions.

In **Chapter 2**, we developed a spatially-explicit capture-mark-recapture framework (SECR) adapted to the multistate formulation to tear apart true survival and permanent emigration in long-lived species. To do so, we jointly estimated survival, natal dispersal, and detection probabilities by appropriately linking a multistate mark-recapture submodel, and a natal dispersal submodel based on information provided by the resighting locations of marked individuals. The structure of the method may be flexible enough to be adapted to different species and study systems. Our results revealed that differences between apparent and true survival may considerably vary by sex, age, and breeding status in long-lived populations. Permanent emigration probabilities were estimated at around 40% in the study population and showed sex and spatial patterns.

In **Chapter 3**, we incorporated the joint-estimation framework developed on chapter 2 into a spatially-explicit integrated population model (SEIPM) to describe the long-term dynamics of the study population. This SEIPM permitted the full description of the four processes that governed population dynamics: Birth, Immigration, Death, and Emigration (i.e., the BIDE processes) along with key vital rates and relevant population stages. Our results showed considerable declines in the study population in Catalonia in the late XXth century followed by substantial recoveries in more recent years. In addition, we obtained valuable information about the temporal variation of all BIDE processes, demographic parameters, and population stages in the declining and increasing phases of population growth. Our findings also revealed new insights about the long-term variations of sink-source status and floater populations in long-lived species.

In **Chapter 4**, we used the estimates of apparent and true survival provided at chapter 2 to compare the outcomes of demographic PVAs when both types of estimates were used, as well as their respective fits to census data. In addition, we explicitly modelled emigration and immigration in models based on each type of estimate to evaluate how these may improve or decrease the fit of each model type. Our results showed that PVAs based on each survival estimate may lead to considerably different, even opposed projections of population viability. In addition, our findings suggested that apparent and true survival may only retrieve population dynamics accurately in specific population scenarios in which emigration and immigration processes match the particularities of each type of estimate. Hence, either PVA calibration, the explicit incorporation of migration processes, and/or modifications in study design may be critical to increase the reliability of PVA projections.

Advances and flexibility in population models: implementations to this thesis

The diverse types of population models used in this dissertation permitted an analysis of population dynamics from different perspectives. The Bayesian spatially-explicit capture-mark-recapture model (SECR) developed in chapter 2 enabled the separate estimation of true survival and permanent emigration probabilities. To do so, our SECR approach required four types of information: 1) tag-resighting data, 2) the locations of the areas of birth (i.e., areas of first capture in this case) and first resighting as breeders of the tagged individuals, 3) information about the population or species range inside and outside the study area (in our case the known or simulated locations of breeding territories), and 4) information about detection probabilities across space (i.e., a definition of which areas were and were not monitored). Models consisted of a multistate CMR submodel and a natal dispersal submodel appropriately linked, so that potential natal dispersal events that ended up in unmonitored areas of the species range could be modelled in the CMR submodel as permanent emigration cases instead of mortalities. Formulating and addressing the interdependence between natal dispersal, detection, and survival probabilities might be complex in many analytical frameworks. However, the Bayesian hierarchical modelling formulation used here permitted the decomposition of the permanent emigration process into the simpler, coupled scaling steps described followingly. First, the modelling of whether an individual may or may not recruit to the breeding population following recruitment probabilities. Second, the modelling of natal dispersal. Third, selection of a breeding territory. Fourth, the assignment of a detection probability depending on the location of the territory (i.e., monitored / unmonitored). Fifth, the modelling of the multistate transition to either an observable or permanently unobservable state. Importantly, this ability of hierarchical models to decompose complex processes into smaller steps has been of great use for representing complex ecological processes and modelling structures in a wide range of ecological studies, as well as in this dissertation (Royle & Dorazio, 2008; Kéry & Schaub, 2012).

As the SECR model was built in the multistate framework, it may be well adapted to long-lived species, where the heterogeneities in vital rates and demographic parameters often need to be accounted for (e.g., in survival, recruitment, recovery, and detection probabilities). An important assumption of the SECR model was that there were no other sources of permanent emigration aside of natal dispersal. This assumption may completely adapt to the study species and other territorial raptors, in which dispersal after first breeding (i.e., breeding dispersal) is rare and may imply distances of only few kilometres that will rarely cause permanent emigration. Because natal dispersal is generally larger than breeding dispersal and is often the main contributor to permanent emigration, this assumption may be satisfied to a reasonable extent in a wide range of species (Matthysen, 2012). However, for species with large breeding dispersal, other spatially-explicit formulations may be more suitable (Schaub & Royle, 2014; Paquet et al., 2020).

Our SECR formulation was implemented in two different scenarios: when 1) resightings from most of the range of the species in western Europe were available (called "JOINT-ALL" models in chapter 2), and 2) resightings were limited to a study area that is relatively small in comparison to the whole range, as is frequently the case in ecological studies (i.e., "JOINT-CAT" models). Overall, the true survival, natal dispersal, and permanent emigration estimates of JOINT-CAT models considerably approached those of JOINT-ALL models, but still showed some visible underestimations. This finding is consistent with those of Schaub & Royle (2014), Dupont et al. (2022), and Efford & Schoffeld, 2022; who showed that the ability of SECR models to totally tear apart true survival and permanent emigration may decrease in parallel to the dimensions of the study area. Essentially, a model's ability to distinguish permanent emigration from true survival may depend on its ability to estimate the true (natal) dispersal kernel of the study population. As the study area decreases in size, so does the probability to detect long-distance natal dispersal movements, which may lead to underestimations of the true dispersal kernel, and subsequent underestimations of permanent emigration probabilities and true survival. Nevertheless, a relevant result of chapter 2 was that the choice of a distribution to model natal dispersal may improve a model's ability to retrieve true survival and natal dispersal probabilities in cases of data limitation. In particular, heavy-tailed kernels like lognormal distributions may more realistically model natal dispersal kernels even if there is scarce data about long-distance movements. A reason for this is that long distance dispersal movements are very frequent, especially in birds, and thus distributions that maintain high expectations at large differences may generally be more accurate. Our findings matched those of Van Houtan et al. (2007,2010), and Fandos et al. (2023), which suggested that heavy-tailed dispersal kernels would be more adequate in a wide variety of bird species. In this respect, our results showed that when heavy-tailed distributions were used, JOINT-CAT models corrected on average 85%, 77%, and 53% of the difference between apparent survival and JOINT-ALL models for non-breeding juvenile, subadult, and adult females respectively, and 87%, 100%, and 78% in the case of males. In terms of area, the focal study population in Catalonia encompasses less than 10% of the size of the western European range of the species. Additionally, the estimated average natal dispersal distances and kernels showed large probabilities of overcoming the dimensions of the study area, with permanent emigration probabilities estimated at ca. 39%. At this level of data restriction, our results look promising, but further research is needed to fully quantify the ability of heavy-tailed distributions to enhance the performance of SECR models for true survival estimation. In addition, taking advantage of the flexibility of Bayesian hierarchical models, the integration of prior data from previous studies or information from telemetry, if available, may also help at the reliable modelling of true dispersal kernels and the subsequent effective separation of permanent emigration from true survival in cases of restricted data. On the other hand, our results suggest that partially retrieved estimates of true survival can still be valuable for the study of population dynamics and applied conservation, as they may already partially inform about whether differences in apparent survival among population stages may be due to variation in true survival or site fidelity. Thus, the use of this approach may provide a more consistent knowledge of the dynamics of study populations.

From a methodological perspective, chapter 3 was based on the integration of SECR methods into spatially-explicit integrated population models (SEIPMs). The insights provided by this analytical framework were deeper than the ones that conventional IPMs alone could have provided. In this respect, the SEIPM formulation permitted an explicit modelling of the four processes that govern population dynamics, that is, the BIDE processes: Birth, Immigration, Death, and Emigration. To date, most IPMs that accounted for migration processes used apparent survival together with immigration (e.g., Abadi et al., 2010; Schaub et al., 2010; Brown & Collopy, 2013; Lieury et al., 2016; but see Weegman et al., 2016; Paquet et al., 2020). In these cases, emigration is accounted implicitly in the models as a part of apparent survival, but this prevents separate modelling of true mortality and emigration. Because SECR models provide estimates of true survival (and thus true mortality) and permanent emigration, the separate magnitudes of both processes along time can be traced. On the other hand, we estimated immigration as a hidden parameter without explicit data as is generally done in IPMs (Abadi et al., 2010). We talked over the validity of this estimation method and the robustness of our immigration estimates in further sections of this discussion. Another important benefit of the use of SEIPMs was their ability to calculate sink-source status and model its dynamics along time. This is particularly favoured by the capacity of SEIPMs to estimate all four BIDE processes, which is a fundamental step towards reliable sink-source estimations (Runge et al., 2006; Furrer & Passinelli, 2016; Heinrichs et al., 2019a). As shown in chapter 3, this framework may be of great use to model and comprehend temporal variations in sink-source dynamics in long-lived species, from which the available knowledge remains scarce (Heinrichs et al., 2016).

In chapters 1 and 4, we developed demographic PVAs grounded on individual-based models, which allowed a fine-scale representation of the Bonelli's eagle life cycle. Sequentially, we represented mortality, aging, recruitment to the breeding population, permanent territory acquisition, mating, breeding, and birth in a sex and age-structured population. In addition, we modelled reintroduction releases in chapter 1, and emigration and immigration in chapter 4. The flexibility of individual-based models to accurately represent the specific characteristics of different study species and scenarios may be critical to obtain realistic population dynamics representations and projections. This point is a main advantage of custom-built demographic PVAs against built-in programmes, which frequently involve less flexible structures (Lacy, 2000; Chaudhary & Oli, 2020). Besides, these levels of modelling flexibility have not been achieved yet in Bayesian-based PVAs, where the development of individual-based frameworks has been a struggle for years, although the first approaches are starting to be developed (see Petracca et al., 2023).

The flexibility of custom-built individual-based models also allowed for multiple additions into the PVAs developed in chapters 1 and 4. For instance, we could simulate releases of eagles by different reintroduction strategies and using different sets of demographic parameters in chapter 1. In addition, we could include a consideration of economic costs into PVA structures. In our case, economic costs were implemented in a rather straightforward way by means of modifying the numbers of individuals that could be released depending on the different budgets available. However, a wide variety of approaches can be designed and modelled to adapt to the specific features of different study systems (e.g., Newbold & Siikamaki, 2009; Kuemmerle et al., 2011, Sebastián-González et al., 2011). Furthermore, in chapter 4, we were able to include emigration and immigration processes at the time of recruitment to the breeding population and territory acquisition, thus adapting to the particularities of these demographic processes in the study species.

Still on chapter 4, the better fit of models based on true survival was probably explained because emigration and immigration tended to be at a certain balance during the study period, 2008-2020. This rationale is supported by the findings of chapter 3, in which the estimates of both processes showed very similar numbers during these years. However, the fit of true survival models probably would have been poorer if emigration and immigration were disbalanced, as shown by our results when migration processes were modelled explicitly. Overall, our results suggested that the modelling of migration processes may be critical to obtain accurate outcomes in demographic PVAs. In this respect, a joint consideration of the results of spatially-explicit capture-mark recapture models (i.e., chapter 2, emigration estimates, true survival if needed) and integrated population models (i.e., chapter 3, estimates of both migratory processes and more precise estimates of demographic parameters) could provide PVAs with more tools to model and project population dynamics with improved accuracy. As a general message for PVA implementation, chapter 4 results suggested that the role of model calibration in improving the confidence in PVA outcomes may be central, especially in cases where reliable information of all 4 BIDE processes cannot be obtained or modelled. These findings add to the claims of the studies from Beissinger & Westphal (1998) and Pe'er et al. (2012), who already evidenced the fundamental role of model calibration for the validation of the modelling structures, life cycle, and stochasticity approaches considered in PVAs.

Overall, in this thesis, the flexibility of widely extended tools like individual-based demographic PVAs, and the recent advances in mark-recapture analysis and integrated modelling in the Bayesian framework, provided an improved capacity to 1) adapt to the particularities of different study systems, 2) fully estimate the main demographic processes that govern population dynamics with simpler or more accessible data requirements, and 3) ease the incorporation and modelling of these processes using flexible structures. The joint consideration of individual-based PVAs, spatially-explicit mark-recapture models, and spatially-explicit integrated population models may provide a deeper knowledge of the dynamics of study populations with central implications for conservation.

General implications for the population ecology of long-lived species

An important focus of this thesis was the estimation of differences between apparent and true survival and their implications for population dynamics and conservation (chapters 2, 3, 4). The use of apparent survival may be problematic when comparing survival estimates between local populations or species, as differences may correspond to variation in permanent emigration instead of actual survival differences. In the particular case of long-lived species, whose survival estimates are usually structured by population stages, intrapopulation differences in apparent survival could also be the result of differences in the magnitude of permanent emigration. The results of chapter 2 support this rationale. Specifically, the differences found between apparent and true survival in the study population considerably varied across age classes, both sexes, and breeding status. First, these differences were larger in females than in males. In relation to this finding, our natal dispersal kernels showed higher dispersal probabilities at large distances for females. These results are in line with the available literature, which shows that female birds generally undertake longer dispersal movements potentially leading to larger permanent emigration probabilities, which could result in larger survival biases (Greenwood & Harvey, 1982; Schaub & Royle, 2014). Importantly, sex-biased patterns of dispersal may be frequent in natural populations (Trochet et al., 2016). In the case of mammals, males generally disperse further. However, in other taxa such as arthropods, reptiles, and fish, sex-biased patterns may largely vary among species, which might make potential sex differences in apparent survival difficult to interpret (Li & Kokko, 2019). Besides, in the study population, differences between apparent and true survival concentrated in the non-breeding fraction. Because natal dispersal is considerably larger than breeding dispersal in most species and across taxa, larger differences in the non-breeding population may be the norm rather than the exception (Matthysen, 2012). Furthermore, our results showed that differences between apparent and true survival may show patterns of age variation specific by sex. The biggest survival differences in males were found in juveniles, while in females these were found in older individuals. These differences were probably related with sex-specific patterns in recruitment probabilities. Males tended to start recruiting to the breeding population earlier than females, while females showed considerably larger recruitment in adult stages. Because recruitment is an indicator of the age of first breeding, it also reflects the age at which natal dispersal is performed. Following this rationale, recruitment estimates (or similar parameters, such as age of first breeding) could provide hints about which age classes may be more affected by permanent emigration. Overall, our results suggest that permanent emigration may affect different population stages in complex ways, and hence, an estimation of true survival in long-lived species may be important to correctly interpret their dynamics.

The magnitude of the differences reported between apparent and true survival in chapter 2 was mild compared to other studies, which were mainly based on relatively short-lived species. In passerine birds – the main focus of these studies so far – Cilimburg et al. (2002), Schaub & Royle (2014), and Paquet et al. (2020) found variations around ca. 0.2-0.3 in females, and 0.1-0.15 in males. In contrast, our differences were of ca. 0.05 – 0.08 in females and 0.01 – 0.03 in males on average, and only in the non-breeding fraction. Importantly, differences of such magnitude may already lead to opposite projections of population viability, as found in chapter 4. Because our studies focused on a long-lived species, even small variations in survival estimates may have relatively large effects on population growth rates (Saether & Bakke, 2000; Hernández-Matías et al., 2013; Chevallier et al., 2015).

The estimation of emigration and immigration was another recurrent topic in chapters 2, 3, and 4. The development of SECR models allowed the estimation of permanent emigration probabilities. This formulation was incorporated into a SEIPM to estimate both the numbers of emigrants and immigrants. The modelling of both migration processes in chapter 4 suggested a central relevance of their estimation for PVA accuracy. The ability of SEIPMs to explicit model all BIDE processes and true survival permitted a straightforward estimation of sink-source dynamics. Sink-source estimation has traditionally been a big challenge in demographic studies because appropriate or reliable data are often not available (Runge et al., 2006; Furrer & Passinelli, 2016). For instance, assessments based on apparent survival without explicit migration information can bias sink-source estimation towards a sink status (Pulliam et al., 1988; Runge et al., 2006; Furrer & Passinelli, 2016). As a result, there is scarce knowledge about how and why sink-source status may vary along time, and most of it is based on theoretical and simulation works (Guo et al., 2005; Heinrichs et al., 2016, 2019a, 2019b). In chapter 3, this modelling framework allowed detecting a shift from a frequent sink to a frequent source functioning along time. Additionally, we could evaluate whether local processes (i.e., births and deaths) or interpopulation movements (emigration and immigration) had a larger influence on local sink-source status. Overall, SEIPMs may provide an ideal framework to understand the drivers and temporal variation of source-sink dynamics.

In chapter 3, we also modelled floater population size along time, which commonly constitutes an “invisible” population fraction in long-lived species. Including non-breeders in integrated population models may be fundamental to obtain unbiased estimates of demographic parameters (Lee et al., 2017; Oppel et al., 2022). Additionally, this population stage can be of central relevance for the dynamics and stability of long-lived populations (Hunt, 1998; Penteriani et al., 2011). Increases in floater population size may lead to increased intraspecific competition with potential negative implications for productivity, as could be the case in our study, but also to increased population stability (López-Sepulcre & Kokko, 2005). The calculation of the floater-to-breeder ratio, as performed in the study, may be a reliable indicator of a population’s buffering capacity against losses in the breeding population (Hunt, 1998). Besides, the role of non-breeders in the expansion of territorial populations is still certainly unknown. Although floaters may establish into new territories, in many cases they may queue for already occupied territories, leading to increased competition. As hypothesized by Hunt (1998), larger accumulations of floaters may promote the creation of new territories in the vicinities of local populations, leading to range expansions. Our results provide indirect evidence supporting this hypothesis, as the estimated large increases in the number of breeding pairs between 2012 and 2020 were preceded by a recovery of the floater population in the 2000s. Additionally, larger intraspecific density due to increases in the floater population may lead to variation in emigration and immigration probabilities. Unfortunately, the relatively limited sample size available limited the degree of detail of our emigration and immigration rates. The ability to jointly estimate all processes provided by SEIPM frameworks in combination with larger amounts of data may provide opportunities to understand the interaction between all these processes and population stages and their implications for the management of territorial and long-lived species.

New insights about the long-term dynamics of the Catalan study population

The implementation of a SEIPM permitted a fine-scale study of the dynamics of the Catalan Bonelli's eagle population for the last 35 years (i.e., 1986-2020). Previous articles had already characterised the dynamics of this population from different perspectives. Between the 1980s and the 1990s, a declining trend in the number of breeding pairs was reported, and additional studies characterised the natal dispersal patterns and main causes of mortality (Real & Mañosa, 1997, 2001; Real et al., 2001). In the 1990s and the 2000s, the population was characterised as a declining sink that received immigrants from southern Spain and required a mitigation of non-natural mortality to revert the population decline (Real et al., 2001; Hernández-Matias et al., 2013, 2015). The findings of chapter 3 constitute a re-evaluation of the dynamics reported in the 1980s, 1990s, and 2000s along with updated information from the 2010s and novel insights on the long-term dynamics of the species: BIDE processes, survival and recruitment probabilities, migration processes, sink-source dynamics, and the population trends of breeders and floaters. Overall, our results suggest that the breeding population declined ca. 25% between 1986 and the early 2000s, followed by a stable period in the 2000s and a rapid recovery in the

2010s towards the initial number of pairs. The estimated initial declines matched the findings of Real & Mañosa (1997) and Hernández-Matías et al. (2013). As a new finding, the floater population was estimated as practically drained until the 2000s, where it progressively increased until reaching ca. 40 individuals on average in 2020. Unfortunately, due to data limitations, we could only estimate non-breeder survival and recruitment probabilities as different between three stages (i.e., 1986-1999, 2000-2007, and 2008-2020), which could have prevented a larger detail in the modelling of yearly variations in the floating population. However, because all these three stages coincide with three different periods of population growth according to census data (decreasing, stable, increasing), these survival estimates may already be capturing temporal variations relatively well. Thus, the estimated variation in floater dynamics is probably quite accurate in the small scale. Given the central role of floater populations in buffering breeder declines in territorial species, the drainage of the floater population might have led to the relatively quick decline observed during the 1990s. The estimated increases in the numbers of floaters in subsequent years would match recent field observations. Before the 2010s, it was extremely rare to observe interferences of floaters in breeding territories, and replacements in breeding territories after mortalities could take weeks or even months. Instead, presence of floaters, persecutions, and even fights with breeders in territories are not uncommon at present. Additionally, whenever a breeder dies, replacements by new individuals in territories are a matter of days (Joan Real, Antonio Hernández-Matías, and Francesc Parés, personal communications). This fact would suggest that the population is now experiencing increased competition for nesting resources, which may also explain the estimated decline in productivity rates along the years (Bretagnolle et al., 2008). However, there may be other feasible and non-exclusible explanations for such productivity declines, such as declines of their main preys – rabbits (*Oryctolagus cuniculus*) and red-legged partridges (*Alectoris rufa*) in the 1980s and early 1990s (Real, 1991; Delibes-Mateos et al. 2009; Moleón et al., 2012). Another explanation may be the colonization of new breeding territories of lower quality as the population increased (Ferrer et al., 2015).

The increases in floater and breeder population sizes occurred in parallel to considerable increases in true non-breeder survival. Between the 1986-2007 and the 2008-2020 period, juvenile survival increased by avg. 0.2, and immature and subadult survival increased by avg. 0.23. Survival of adult non-breeders was estimated together with immatures and subadults for the period 1986-1999. However, due to the reported high recruitment and low survival rates, the presence of adult non-breeders was anecdotical. Even so, survival of this fraction reached avg. 0.86 between 2008 and 2020. The considerable retrofitting efforts in power lines from the 2000s onwards, along with the possible reduction of other threats like direct persecution, may be behind these large survival increases (Chevalier et al., 2015; Hernández-Matías et al., 2015). Interestingly, according to the results of chapter 4, even smaller increases in non-breeder survival could have led to increases in population growth compatible with reversions of population declines (avg. 1-3% in males combined with 5-8% in females, varying by age class). Hence, the observed increases could have been determinant for the recovery of the population. On the other hand, an apparently small trend towards an increase was only found for breeder survival (ca. 2-3%). However, this parameter showed the largest influence on population growth rates, as is common in long-lived populations, suggesting that even small changes in breeder survival could have sensible impacts in population dynamics. In Chevallier et al. (2015), where similar sensitivities and elasticities were found in the closely related Bonelli's eagle population in France, an increase by 0.03 in adult survival already had the potential to revert the observed population decline. Even though our breeder survival estimation was quite precise, such small increases may not be reliably detected with the present uncertainty associated with our estimates. Hence, a central role of adult survival in the recovery of the population may not be discarded. This fact may illustrate the fine scale at which long-lived population dynamics, which may require considerable precision from models and data.

The Catalan population also showed long-term variation in migration patterns along time. Immigration was the larger process in the population in the 1980s, 1990s, and 2000s, but it reached a balance with emigration in the 2010s. While the effect of both processes in population growth and local sink-source status appeared to be limited, immigration probably played a critical role in buffering breeding population declines in the 1990s and 2000s. In fact, the number of immigrant recruits was considerably larger than that of local recruits for most of the declining and stable phases of population growth. This result mimicked the findings of Lieury et al. (2016) for the neighbouring French population at the same period. Nevertheless, as both the Catalan and the French population started recovering in the late 2000s, immigrant recruits decreased in numbers and proportion in Catalonia, while they remained stable in numbers in France.

Overall, the sustained population increases in France and Catalonia during the 2010s contrasted with considerable declines in other populations in the western European range of the species. Populations in eastern and northern Spain with formerly stable or increasing populations suffered marked declines (i.e., Valencia, Aragon, Castilla la Mancha). Northern populations showed contrasting trends (declines in Navarra and the Basque Country, increases in the northwest and the northeast), and southern populations remained rather stable (Andalusia, Extremadura, Murcia). An updated assessment of source-sink dynamics would permit comparisons with previous evaluations (Hernández-Matías et al., 2013), and thus help at understanding the functioning, temporal variation, and environmental drivers of this spatially-structured system with wide implications for sink-source research.

Implications for wildlife conservation

Aside of the methodological and demographic perspectives of this thesis, our results may also have meaningful implications for the conservation of the local population, territorial raptors, and long-lived animals in general. The results shown in this dissertation emphasized the relevance of generating evidence-based knowledge about the effectiveness of conservation actions. The availability of these types of analyses may favour the movement from traditional conservation built on a feel-belief basis to scientific approaches based on the analysis of quantitative data. In chapter 1, we found that the translocation of wild non-juveniles may be a cost-effective option to captive-breeding programmes and the widely used hacking method. Interestingly, the improved results of relocations were associated with increases in the rates of recruitment to the breeding population. Because non-juveniles may establish breeding pairs more rapidly, reproduction in the starting years of a reintroduction may constitute an additional source of population gains that may subsequently decrease probabilities of extinction. Instead, the hacking method often implies the release of chicks, which in long-lived species may imply several years until individuals start reproducing. In this respect, our results built on the findings of Morandini et al. (2019), who acknowledged the relevance of considering not only the demographic effects of survival in reintroductions, but also those of recruitment probabilities. Nevertheless, the discussion of chapter 1 also emphasized the variable nature of reintroductions and study sites and the pros and cons of different release strategies. In this sense, embracing adaptive management - the continued monitoring of the population accompanied quantitative evaluations of the success of conservation decisions and modifications based on their results – may be key to ensure reintroduction success (McCarthy & Possingham, 2007).

The findings of this dissertation also examined the general assumptions and performance of demographic PVAs. Thus far, several concerns have been raised about the capacity of issues like poor representations of intrapopulation heterogeneity in life cycles and demographic parameters, and simplistic or wrong treatments of uncertainty and stochasticity, to wrongly affect the results and reliability of PVAs (Beissinger & Westphal, 1998; Reed et al., 2002; Chaudhary & Oli, 2020). The findings of chapters 2 and 4 suggest that another source of concern that has been traditionally overlooked should be added to the list (Zimmermann et al., 2007). Specifically, the type of survival used and the effect of permanent emigration in apparent survival estimates could have a significant influence in PVA projections, and subsequently, in conservation decision-making. Apparent and true survival will generally be different in wild populations due to the extended presence of permanent emigration, thus potentially leading to different PVA outcomes. The results of chapter 4 are a good example of this, with true survival leading to a population increase and apparent survival leading to a decline. Additionally, apparent survival may be larger or lower depending on the magnitude of permanent emigration in the study population. This magnitude will often depend on 1) the size of the study area, and 2) the dispersal capacity of the study species (Zimmerman et al., 2007; Horton & Letcher, 2008, Chadoeuf et al., 2017). Thus, apparent survival may generally be lower in study designs that encompass small study areas, and/or in populations with larger dispersal capacities. Hence, interpretations of apparent survival estimates from CMR studies and PVA projections based of these estimates should consider the magnitude of these factors. Otherwise, managers might be at risk of systematically underestimating the projections of populations with large dispersal capacities or restricted study/monitoring designs. At the same time, the effectivity of both apparent survival and true survival at retrieving realistic population dynamics may depend on the dimensions and equilibrium between emigration and immigration processes. While true survival may fail at projecting realistic PVA outcomes if migration processes exceed one another, apparent survival may systematically underestimate population trends if immigration is present in a study population. Because information about these processes is rarely available for PVAs, it may be hard to understand if the survival estimates used may be adequate for PVA modelling. Based on this, a potential way of assessing their suitability may be to perform model calibrations to census data to visualize the fit of PVA predictions, as done in chapter 4. One further solution previous to the start of data collection may be to modify study designs to either i) enlarge study areas to limit the effect of migration processes on survival and population dynamics, or ii) obtain data that allow the estimation of emigration and immigration. In this respect, the development of SECR models (chapter 2) and IPMs and SEIPMs (chapter 3) enable the estimation of these processes with simpler data requirements (Abadi et al., 2011). Otherwise, telemetry data may also provide valuable information about these processes.

Overall, the results of this dissertation emphasize how novel population modelling frameworks such as Bayesian SECR and SEIPMs can provide deeper insights into the field of conservation biology. In the Catalan study population, the observed rise in non-breeder survival and subsequent increase in the floater population was probably due to active conservation action in the study area (although other environmental changes such as increases in prey availabilities cannot be discarded). Importantly, non-breeder and breeder fractions of territorial populations often do not coincide in the same areas, as is the case of the Bonelli's eagle (Real & Mañosa, 2001). While breeders stay in territories most of the time, non-breeders often exploit areas away from territories with large prey availabilities (i.e., dispersal areas). The joint management of both areas in species with such differences in space use among population stages may be crucial to improve their conservation status (Penteriani et al., 2011; Hernández-Matías et al., 2015). In the study population, power line retrofitting actions were implemented in both areas, which may help explaining the observed improvements. Importantly, the increasing floater abundances should rather be regarded as positive for the Catalan population. While floaters could indeed have negative effects on the productivities and even the survival of breeders, these are unlikely to offset the benefits provided by the increase buffering capacity and stability of the population (Newton, 1988; Hunt, 1998; López-Sepulcre & Kokko, 2005; Bretagnolle et al., 2008; Penteriani et al., 2011). Additionally, large floater accumulations may enhance the expansion of the population towards new breeding territories and promote emigration to neighbouring populations (Hunt, 1998; Matthysen, 2005). Further conservation action targeted at mitigating mortality may also strengthen the role of the Catalan population as a source (Heinrichs et al., 2019b). In this respect, managers and practitioners should now be aware of the likely functioning of the Catalan population as a source in recent years. Thus, the management of the Catalan population may also be positive to buffer the observed declines of neighbouring populations, such as Aragon and Valencia, and maintain the sustained increases in the French population in the last decade (Lieury et al., 2016). Overall, we believe that the findings of chapter 3 may illustrate the benefits of long-term monitoring and sophisticated data analysis to generate conservation knowledge for managers and practitioners and encourage the systematic implementation of these methodologies in this and other populations in future years.

Assumptions and limitations of this thesis

Obtaining large sample sizes for the study of long-lived populations may be critical due to their complex life cycles and intrapopulation heterogeneities. However, this may be challenging as it often implies the monitoring of relatively small populations, especially if they are threatened. In addition, the monitoring of individuals throughout their lives may imply intensive efforts during several years or even decades. The demographic datasets available for the Catalan population were obtained from intensive monitoring schemes, especially in the 2008-2020 period in which up to 70% of the population was ringed and ca. 70-80% of all breeding territories were surveyed to obtain reproduction and territory replacement data. Even with this, the sample size available was still limited at the time of estimating some demographic parameters of interest at full resolution. For instance, fixed estimations of non-breeder survival, recruitment probabilities, permanent emigration, and immigration rates for three different time periods were necessary (chapters 2 and 3). While this fact enabled an understanding of the main variation of these parameters in different periods of population growth, it prevented a complete consideration of yearly variations. Additionally, our fixed non-breeder survival estimates prevented a full decomposition of sampling and temporal variance for the PVAs of chapter 4. Separating both variances is the most accurate way to model demographic parameters along time and propagate uncertainties into the models (McGowan et al., 2011). As a solution, our selected structure consisted in incorporating parametric uncertainty as a whole. This might be the best option available in our case, compared to using point estimates or assuming variances from other populations (which were not available either for non-breeder survival).

Importantly, in most cases where the data available were not of enough resolution to estimate specific demographic parameters or could be subjected to potential biases, the extensive knowledge available on the species and the study populations either provided certain evidence or safety to justify the values obtained in the estimations, or permitted the use of demographic parameters obtained by other methods or in other populations with similar conditions (Real and Mañosa, 1997, 2001; Real et al., 2001, Hernández-Matías et al., 2010, 2011a, 2013, 2015;). This particular condition of the study species was advantageous for this thesis, and is the result of intensive, long-term monitoring and research efforts. In this respect, the mark-resighting dataset for the Catalan population from 1986 to 1999 included fewer amounts of individuals and was subject to tag loss (chapter 3). We used a multistate structure to account for tag loss in the estimation of demographic parameters (Badia-Boher et al., 2019). Additionally, the estimates of demographic parameters and tag loss were similar to those obtained by other methods in Real and Mañosa (1997) and Real et al. (2001). Also in chapter 3, we assumed survival and recruitment data from the neighbouring Bonelli’s eagle population in France for the period 2000-2007, as no mark-resighting schemes were active for that period (Hernández-Matías et al., 2011a). We are confident that these estimates were likely similar to those in Catalonia for the same period. First, because both populations showed quite similar dynamics along time based on census data, and are continuously distributed along the Mediterranean coast, which altogether may reflect similar environmental conditions and levels of mortality threats between them. Second, because non-breeder survival and recruitment estimates from the French population were already assumed for the modelling of the Catalan population in a similar period (1990-2005), and provided a good fit to the observed population trends in the area. Indeed, most estimates from France showed intermediate values between those of 1986-1999 and 2008-2020, which makes sense with the observed stable phase between the population decline and the subsequent recovery in the study area. In this respect, we took advantage of the possibility of incorporating these estimates along with their associated uncertainties as prior beliefs in the Bayesian SEIPM (McCarthy and Masters, 2005). A detailed evaluation of the suitability of estimates from the French population can be found in chapter 3.

The monitoring data available for the Catalan population did not contain any direct information source from which to infer immigration explicitly. This is common in most study systems due to the considerable challenges of obtaining this type of data. Hence, in chapter 3 we estimated immigration as a hidden parameter using the indirect information provided by other ecological datasets, as is commonplace in IPMs (e.g., Abadi et al., 2010; Schaub et al., 2010; Brown and Collopy, 2013; Lieury et al., 2016). This type of estimation assumes that information about immigration is contained in the difference between the observed population counts and the estimated population numbers by the model. Because this difference may be caused by factors other than immigration, this type of estimation could be biased in some scenarios (Riecke et al., 2019; Paquet et al., 2021; Plard et al., 2021). For instance, if processes that add or remove individuals to the population are ignored (i.e., birth processes, mortalities, emigration, tag loss) immigration estimates may actually reflect any of these processes instead of true immigration. Additionally, immigration estimations based on fixed parameters may be at risk of overestimating the contribution of this process to population dynamics (Paquet et al., 2021). In chapter 3, we carefully accounted for all processes leading to population losses and gains, such as tag loss whenever it was present (period 1986-1999), emigration, productivity, and age and stage-structured survival. Because of the limited data available, we had to estimate immigration as fixed within, but variable between, three different periods that reflected different stages of population growth reasonably well. Our immigration estimates showed that this process was more relevant than emigration in the

1990s and 2000s, which matched the estimates of Hernández-Matías et al. (2013). Additionally, immigration data was also available for the neighbouring French population for the same period (i.e., 1991-2013; Lieury et al., 2016). The results for the Catalan and French populations showed very similar ratios between local and immigrant recruits. These matched findings may suggest that our immigration estimates were reliable, and overestimations, if any, could have remained low. Thus, inferences made from the interpretation of this parameter are probably valid. Furthermore, ignoring immigration as a process may also lead to issues with integrated population models (Riecke et al., 2019; Plard et al., 2021). Because this process provides gains to the population itself, ignoring it may lead to biases in survival and productivity. Hence, we believe that our estimation of immigration is a positive contribution to the model in any case.

The availability of extensive knowledge about the Bonelli's eagle's population dynamics was also central to make modelling decisions in chapter 1. The tag-resighting dataset available for the population in Mallorca was small, as is the general case for recently reintroduced long-lived populations. Thus, model selection was not only based on AICc criteria, but also on the similarities between model results and the well-known demographic features of long-lived raptors, such as age increases in survival (Hernández-Matías et al., 2011a). Productivity estimates were also obtained from a very small sample size but could be validated using comparisons with data from all monitored populations in western Europe (Hernández-Matías et al., 2013). Additionally, integrated models performed in 2021 with larger data availability for the Mallorcan population (2011-2021) showed very similar demographic estimates for all release strategies and age classes, although with less associated uncertainty (Hernández-Matías et al., 2021, technical report; Figure 1). Namely, mean survival was estimated at avg. 0.5 for the first years of hacking and relocation releases (in chapter 1: avg. 0.52 and 0.48 respectively), and mean adult productivity was 1.13 (in chapter 1: 1.2).

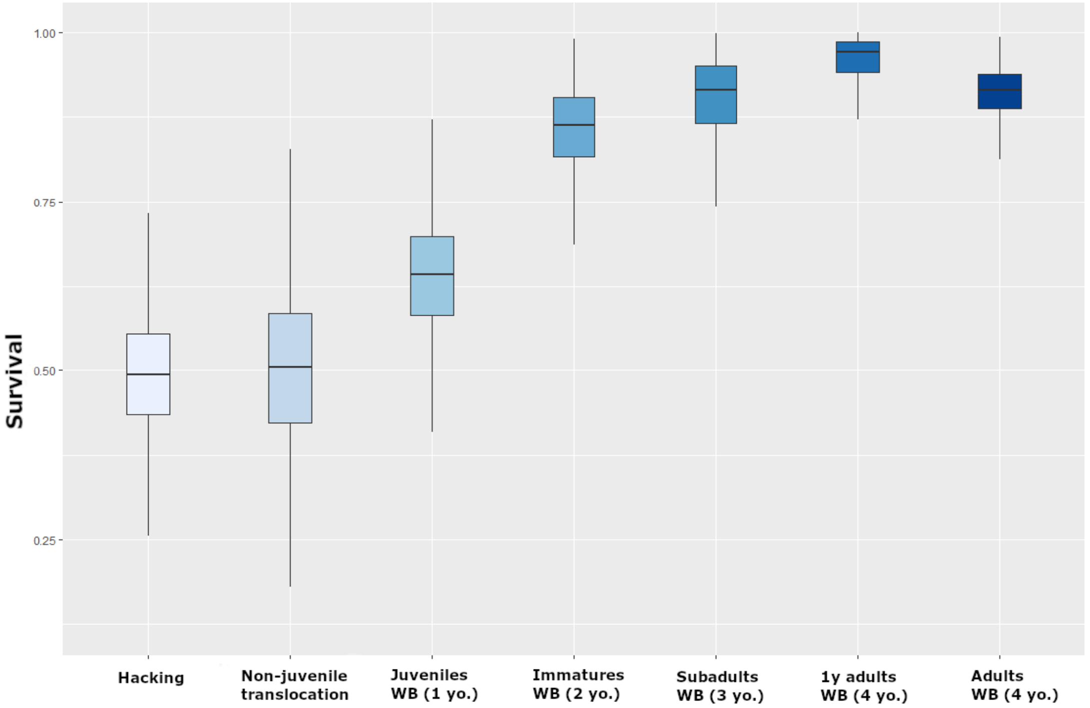

Figure 1. Stage-structured survival estimates for the reintroduced Mallorcan Bonelli's eagle population (2011-2021) published at Hernández-Matías et al. (2021, technical report). Hacking and non-juvenile translocation estimates refer to the first year after release. Abbreviations "WB" and "yo." stand for "Wild-born in the reintroduction area" and "years old" respectively. Boxes indicate the median and the 25%-75% interpercentile range of values of posterior samples. Whiskers reach minimum and maximum sample values, excluding outliers.

Recruitment probabilities were estimated by age but not by release method, which prevents any comparisons, but showed an age-structured variation similar to the differences between eagles released as juveniles and non-juveniles. Hence, this provides solid arguments for the validity of the estimates used and assumed in chapter 1.

Future perspectives in population modelling and potential applications to the study population

As shown in this dissertation, using different population modelling tools may be essential to gain relevant local and general demographic and conservation knowledge from different perspectives. The advent of Bayesian hierarchical models to the field of population ecology keeps providing continuous advances in the study of wild populations (Royle and Dorazio, 2008; Kéry and Schaub, 2012; Kéry and Royle, 2016, 2020; Schaub and Kéry, 2021). In this respect, integrated models constitute opportunities to deal with the often limited sizes of ecological datasets for the study of long-lived species. Based on the combination of different sources of information, demographic estimates and inferences on population trends may achieve larger levels of precision (Schaub and Abadi, 2011). In this respect, while mark-resighting schemes are widely used in IPMs, data from unmarked individuals should always be considered as an alternative and potentially relevant source of demographic information. In integrated population models, count and productivity data are central and most often included in analyses. In the Bonelli's eagle and other territorial raptors, breeder survival estimates may be obtained without the need for ringing schemes if the species is age-characterizable (Hernández-Matías et al., 2011b; chapter 3). Besides, additional unmarked data may be available, such as those arising from occupancy modelling (Kéry and Royle, 2016, 2021). While occupancy data are often not considered in IPMs, these may be relevant sources of information, for instance, about population sizes, territory occupancy, and dispersal patterns (Mackenzie et al., 2003; Kéry and Schaub, 2012; Sutherland et al., 2014).

On the other hand, integrated population models are starting to show their potentialities at analysing more than one species jointly (Queroue et al., 2021). While population models have traditionally focused on studying the dynamics of single species and the intraspecific drivers of population dynamics, the role of other species in terms of predator-prey dynamics, competition, and disease-spreading, may also be determinant. Additionally, the inclusion of multiple populations of the same species can be an opportunity to advance in the understanding of the dynamics of spatially-structured (Paquet et al., 2021). Overall, the flexibility of integrated population models may be fundamental to continue disentangling population dynamics at unprecedented levels of detail.

At the local scale, the increases in the study population in Catalonia may generate new research opportunities and management challenges with relevant implications for long-lived populations. For instance, the estimated increases in the floater population may constitute an ideal case to study the role of floaters in population stability and intraspecific competition. There are still considerable gaps in the fields of floater population dynamics and their demographic roles (Hunt, 1998; Penteriani et al., 2011). Here, the floating population can be studied from a period where it was practically drained (i.e., the 1990s and the early 2000s) to present times, where the floater population is showing an increasing trend and the first signs of strong competition with breeders (unpublished data). Besides, as environmental conditions and human societies change, new threats to the population and the species may appear. For instance, the expansion of other eagle populations in the Iberian Peninsula may be causing increased competition and range modifications in the Bonelli's eagle (López-López et al., 2007). The study of this phenomenon may be of great interest to understand interactions between raptors and the effects of particular species on the trends and demographic parameters of each another. In this respect, multispecies integrated population models may be powerful tools to be considered along with methods that may allow the study of unmarked populations, if any of the species is not tagged (e.g., multispecies occupancy models; Devarajan et al., 2020). Additionally, the expansion of renewable energies, such as wind farms and solar parks, could have important implications for the prospects of the population and may deserve additional assessments (Serrano et al., 2020; Pérez-García et al., 2022). Moreover, the role of changes in land use, the expansion of intensive farming, and the advancing climate crisis on the present and future trends of the species in western Europe deserve further understanding (Donázar et al., 2016; Martínez-Ruiz et al., 2023; Rigal et al., 2023).

As a final consideration of this dissertation, we would like to emphasize the importance of data collection as a pillar for advances in the study of population dynamics and applied conservation. Progresses in any of these fields will probably require increased amounts of ecological data, and hence the implementation of long-term intensive monitoring schemes. Additionally, the availability of high-quality data may favour the integration of advanced quantitative methods in species/population assessments and conservation planning, which may be fundamental for the implementation of effective management actions (Bakker & Doak, 2009). The study populations evaluated in this dissertation constitute encouraging examples of the strong links between population monitoring, the analyses of the resulting ecological data with sophisticated statistical tools, and the resulting capacity to obtain demographic and conservation insights with local and general implications for other species and populations. The collection of these data could never have been possible without the priceless effort, passion, and tight collaboration between monitoring teams, rangers, technicians, volunteers, and public administration members.

We believe that these are central pillars in the success of this and every successful long-term wildlife monitoring project, and will be fundamental for generating new evidence-based conservation knowledge and mitigating the effects of the ongoing biodiversity crisis.

Conclusions

1. In recent decades, population models have made significant advances in sophistication and flexibility. One notable development is the emergence of Bayesian hierarchical models, which are enabling easy integrations of diverse ecological and demographic data. This integration facilitates the estimation of key vital rates and demographic processes whose quantification has been historically challenging. Additionally, individual-based population viability analyses (PVAs) offer a highly flexible framework that aids in generating evidence-based knowledge for wildlife management. In this thesis, the combined use of these two methods showed great potential for providing valuable insights into population dynamics and conservation from multiple perspectives.

2. Spatially-explicit capture-mark-recapture methods enabled the estimation of permanent emigration and true survival probabilities as distinct parameters. These models required multistate mark-resighting data along with the locations of birth and first reproduction of marked individuals, and assumed that all permanent emigration was caused by natal dispersal. The adaptation of this formulation to the multistate mark-recapture formulation provided a flexible formulation for the estimation of these parameters in a wider range of species.

3. Underestimations of true survival by apparent survival varied by age, sex, and breeding status in long-lived populations due to the differential effects of permanent emigration across population stages. Thus, the interpretation of differences in apparent survival across population stages could be problematic, especially when intended at drawing conclusions about population dynamics and conservation action. Hence, in these cases it may be fundamental to estimate true survival.

4. In cases where resighting data were not available from the whole range of a population, spatially explicit capture-mark-recapture models could not separate true survival from permanent emigration completely. In these cases, the use of heavy-

tailed distributions to model natal dispersal kernels enhanced the performance of the models. Additionally, the use of prior dispersal information or telemetry data could help ensuring an effective separation of both processes.

5. Integrating spatially-explicit capture-mark-recapture models within spatially explicit integrated population models enabled the estimation of demographic processes that are often difficult to quantify in other modelling frameworks. Namely, these models permitted the separate modelling of the four processes governing population dynamics: birth, immigration, death, and emigration. This fact facilitated an estimation of sink-source dynamics along time, which is otherwise challenging to achieve in many other analytical formulations.

6. Spatially explicit integrated population models provided valuable information about the long-term dynamics of the Bonelli's eagle population in Catalonia. This population experienced a considerable decline in the 1990s, followed by a recovery in the 2010s. This fluctuation was especially noted in the breeding population. Furthermore, the floater population had been nearly depleted in the 1980s and 1990s, and exhibited substantial increases afterwards. The population's recovery was likely driven by increases in survival, potentially resulting from conservation action aimed at mitigating mortality threats. Between 1986 and 2010, immigration emerged as the predominant dispersal process, while a balance with emigration was achieved thereafter. The population shifted from an average sink to a source functioning in the 2010s.

7. The use of either apparent or true survival in demographic population viability analyses had large impacts in their projections. Particularly, both estimates could only retrieve accurate projections of population dynamics in scenarios where emigration and immigration match the particularities of each type of estimate. Overall, the estimation of emigration and immigration may be critical for reliable PVA projections. However, because information on these processes is rarely available, it may be fundamental to calibrate survival estimates against observed data to test their adequacy. Otherwise, the use of spatially-explicit methods as the ones presented in

this dissertation could help at obtaining estimates of emigration and immigration, which can be readily incorporated into PVAs.

8. In raptor reintroductions, the practice of extracting of non-juvenile individuals from wild populations to relocate them to the release area enhanced reintroduction success in comparison to widely-implemented, resource-demanding strategies such as captive breeding and the hacking method. The primary advantage of relocations was that they enhance early reproduction in the reintroduction area, which could rapidly promote population growth. This fact underlined the important role of breeding status and recruitment processes for reintroduction success.

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The Bonelli's eagle

Aquila fasciata

The Bonelli's eagle has a fragmented Distribution across the Southern Paleartic and Indomalayan regions. It is locally rare and in decline across its range. In western Europe, the species has a generally continuous distribution from southern France and across the Mediterranean coast to southern Portugal, although its range becomes patchy at the western and northern edges. Some populations can also be found in Mediterranean islands: Mallorca, Sardinia, Sicily, Crete, and Cyprus. The eagle's prey mainly includes small or medium-sized birds and mammals, along with some reptiles and insects. It may be found nesting on remote cliff ledges or in large trees.

White coloured breast with a variable amount of sparse blackish-brown streaks

Wing tips moderately fingered for such a large raptor

Grey tail with obscure darker brown thin bars and a broad black terminal band