

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

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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 biases. This study addresses two general but overlooked related issues in PVAs that can significantly affect the reliability of their projections. First, we examined the effects of using apparent 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 PVAs structured by age, sex, and breeding status using as a study system a threatened raptor population (Bonelli's eagle, *Aquila fasciata*) from which apparent and true survival were available (2008–2020). The performances of PVA projections based on each survival type and dispersal process were assessed by evaluating their fit to census data. Our findings revealed that using apparent survival underestimated census data, while true survival showed a considerably better fit. However, models including dispersal processes showed that each survival type may only deliver precise projections at very specific levels of emigration and immigration. Given the potentially large differences found when using true and apparent survival, we suggest that the relevance of this issue should be elevated to that of other widely reported PVA limitations. Recently developed, accessible analytical methods may permit an easier estimation of true survival and dispersal processes. Otherwise, calibrating projections against observed data may be fundamental to test the adequacy of survival estimates.

1. 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 and 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 and Doak, 2002; Chaudhary and Oli, 2020). 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 and Westphal, 1998; Coulson et al., 2001; Reed et al., 2002; Chaudhary and Oli, 2020). Such concerns are mainly

related to 1) the use of poor-quality demographic data, which may lead to imprecise demographic estimates, and subsequently, too uncertain PVA outcomes (Beissinger and Westphal, 1998; Coulson et al., 2001), and 2) an inadequate modelling of uncertainty and stochastic population processes, which may lead to biases and/or overconfidence in PVA outcomes (Morris and 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 and 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 and Oli, 2020). In

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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/productivity and survival estimates respectively, while most designs do not explicitly account for emigration and immigration processes (Morris and Doak, 2002). This approach is frequently taken for convenience as information about dispersal processes is rarely available (Williams et al., 2002). However, wild populations closed to migratory fluxes are the exception rather than the norm (Hanski, 1999; Matthysen, 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). PVA structures that incorporate emigration and immigration processes exist and are known as metapopulation PVAs or spatially-explicit PVAs (e.g., 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 (Lindenmayer et al., 1993).

Survival is frequently the parameter with the largest influence on population growth rates (Sæther and 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). CMR analyses provide two types of survival estimates: true and apparent survival. While true survival (S) purely reflects an individual's probability of survival, apparent survival (ϕ) is the product of true survival and site fidelity (White and Burnham, 1999). Hence, in populations where permanent emigration from the study area exists (i.e., site fidelity is lower than 1), apparent survival is lower than true survival (Marshall et al., 2004; Schaub and 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 and Burnham, 1999). In the last decades, a number of novel CMR methods are facilitating the estimation of true survival, namely, those using information on dead recoveries outside study areas and secondary sampling periods (Burnham, 1993; Lindberg et al., 2001; Dupont et al., 2021; Wood et al., 2021), and more recently, those incorporating explicit dispersal data (Gilroy et al., 2012; Schaub and 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 and Westphal, 1998; Brook et al., 2000; Reed et al., 2002; Chaudhary and Oli, 2020). Additionally, the effects of survival choice on PVAs may be wider (Fig. 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., $\text{Emigration} - \text{Immigration} = 0$), so that population dynamics basically depend on birth and death processes. In any other situations, this parameter may also lead to imbalances between the true and the modelled dynamics.

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 (Chaudhary and 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 dispersal 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 *Aquila fasciata* 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 and Mañosa, 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 dispersal processes and representing the relevant processes in the life cycle of the species (i.e., mortality, birth, recruitment to the breeding

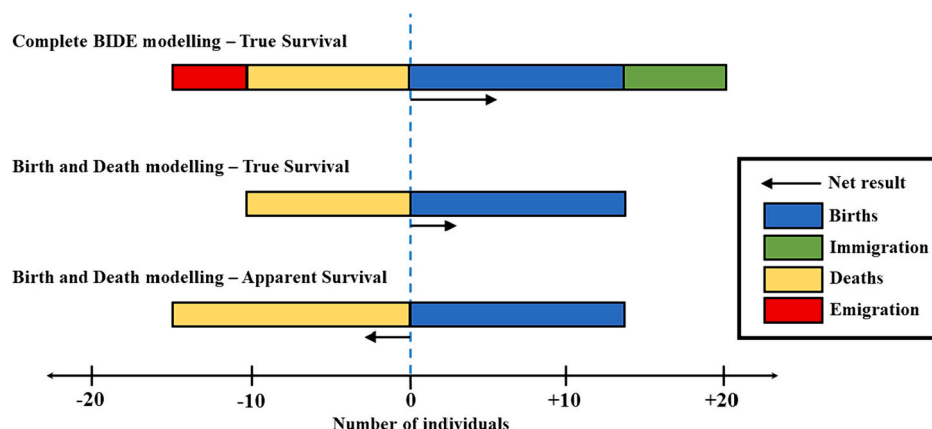


Fig. 1. Example of the potential effect of the type of survival use on the modelling of population dynamics in Population Viability Analysis. This case reflects a population where immigration slightly exceeds emigration and births exceed deaths. The complete modelling of all four BIDE processes (i.e., Birth, Immigration, Death, Emigration) would predict a population increase. The use of true survival without any explicit modelling of dispersal 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.

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 each 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 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, including model calibration to observed data and the explicit estimation of dispersal processes.

2. Methods

2.1. 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. 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 and Mañosa, 2001). 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 and 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).

Here, we use data from an intensive tagging and resighting programme (2008–2020) on the local population in Catalonia, located at the north-east of Spain between the French border in the north and the southern limits of the Ebre Delta in the south (boundary coordinates: N 42.4641, 1.8442; S 40.5323, 0.4812; W 41.6779, 0.3353; E 41.9479, 3.2179). In total, 461 chicks born in 51 different territories were ringed in their nests with metal and alphanumeric anodized aluminium colour rings. All rings were riveted to avoid tag loss. Intensive monitoring efforts were devoted to resighting marked non-breeders across dispersal areas of the population (Real and Mañosa, 2001), breeders in 76 different breeding territories, and dead individuals in breeding territories, dispersal areas, and zones of high mortality risks (i.e., power infrastructure, ponds). In total, 177 birds were resighted at least once, of which 83 were seen recruited as breeders, and 75 found dead. In addition, breeding territories were monitored during the breeding season (yearly mean: 55) to assess productivity. More detailed summary data about the monitoring programme can be found in Appendix A; Tables A.1 and A.2.

2.2. 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) (Table 1). For non-breeders, survival was estimated differently for juveniles (1 year old), immatures plus sub-adults (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

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 in Badia-Boher et al., 2023). Estimates are reported as posterior means and 90 % credible intervals.

Estimate	Age	Sex	Apparent survival	True survival
Non-breeder survival	1 year old	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 years old	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)

ages, which is reasonable considering the reported behaviour 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 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, which leads to increased emigration probabilities. 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 as in most birds, Bonelli's eagle females show larger dispersal distances than males, leading to higher permanent emigration probabilities (Pusey, 1987; Schaub and Royle, 2014).

2.3. Productivity estimation

To model reproduction and birth processes, we estimated productivity as the number of fledged chicks per breeding pair. 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 (Schaub and Kéry, 2022):

$$J_t = \text{Poisson}(R_t * \text{prod}_t)$$

in which the yearly (t) number of fledged chicks *J* was the product of the yearly number of monitored breeding pairs *R* and our yearly productivity estimate *prod*. For this calculation, we used a Bayesian hierarchical modelling approach using package JAGS (Plummer, 2017) in R 4.3.1 (R Core Team, 2023). We ran models in 4 chains for 160,000 iterations of which we discarded the first 110,000.

2.4. Demographic population viability analysis

We built an individual-based PVA 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 and 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 et al., 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 following Morris and Doak (2002). Senescence was incorporated by reducing survival probabilities to 50 % in individuals aged 20 years and older following observed and reported age expectancies of the species (own data; Newton, 1979). 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 is 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 breeder census data in the study population. We added this limitation for biological realism, as the formation of new territories most often occurs at a slow pace along time, as it is 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). 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.

2.5. PVAs incorporating emigration and immigration

In these models, we focused on modelling permanent emigration (hereafter, “emigration”) and permanent immigration (hereafter, “immigration”) respectively. In Bonelli's eagles, as in other territorial raptors, emigration and immigration practically always occur at the time of natal dispersal, as once individuals start breeding, they 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, following the biology of the species, 1) we modelled emigration as the removal of individuals ready for recruitment to a breeding territory, and immigration as the addition of new individuals as potential recruits, and 2) we set the emigration and immigration probabilities of all individuals to 0 after first breeding. The sex of the leaving or newcomer individuals was modelled assuming an equal sex ratio. When using true survival, we set emigration and

immigration to one, three, five, seven, and nine individuals. Instead, for apparent survival scenarios, we only modelled immigration, as apparent survival already accounts for permanent emigration from the study population implicitly.

2.6. Model settings and evaluation of results

As described previously in the introduction, we ran 1) true and apparent survival PVAs without an explicit modelling of dispersal processes for the period 2008–2020, 2) the same models 30 years into the future (2020–2049), and 3) true and apparent PVAs including dispersal 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 10,000 replicates. Models were built using R 4.3.1 (R Core Team, 2023) and using functions of package PopBio (Stubben and 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 geometric mean of the population growth rate: $\left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}$, where N_t is the final number of breeding pairs, N_0 is the initial number of breeding pairs, and superscript t is the number of years of the census time series (Morris and Doak, 2002). Then, we assessed each model's probability of retrieving λ_o given their set of predicted lambdas (λ_c). 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 de Oliveira et al., 2016). 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. PVA projection results were reported as the mean and corresponding 90 % interpercentile range between 5 and 95 percentiles (hereafter referred to as the 90 % confidence interval, 90 %CI).

3. Results

3.1. 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.

3.2. No explicit modelling of dispersal 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 size of the population, although this was permanently inside the 90 % range of predicted trajectories of the true survival model (Fig. 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.

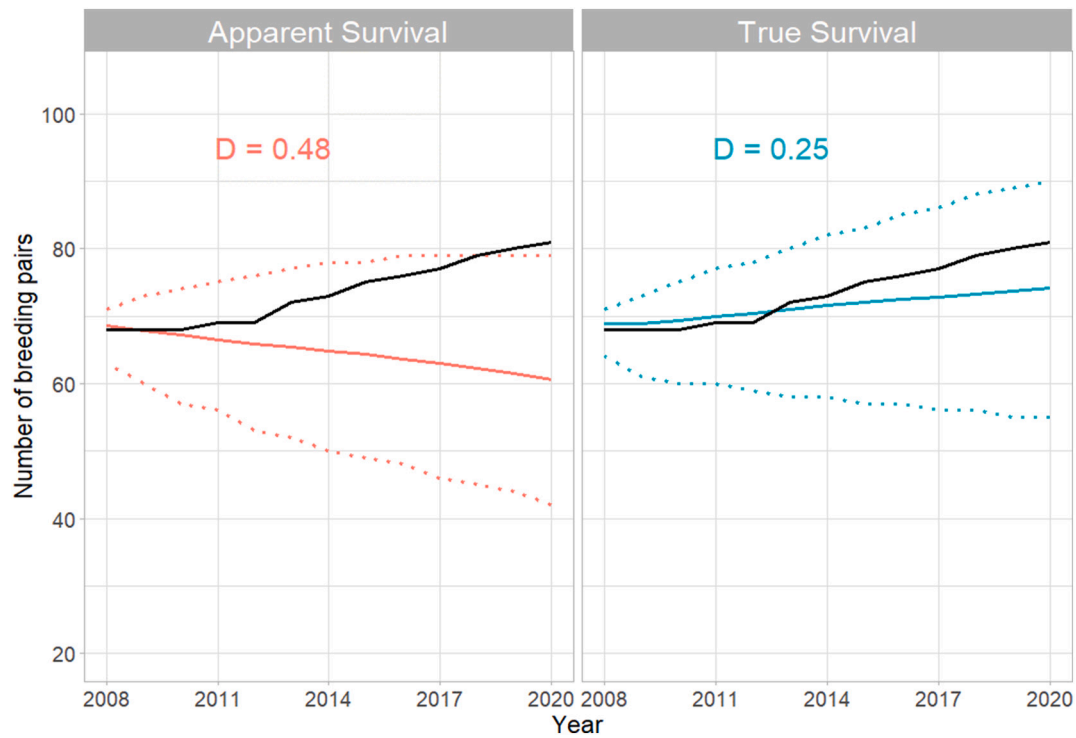


Fig. 2. Means (coloured solid lines) and 90 %CIs (dotted lines) of the numbers of breeding pairs projected by the PVAs between 2008 and 2020 under the use of apparent and true survival. Black lines indicate the observed numbers of breeding pairs in the study population from census data. Parameter D shows the fit of census data to PVA projections. Values closer to 0 indicate a better fit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. No explicit modelling of dispersal 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 (Fig. 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

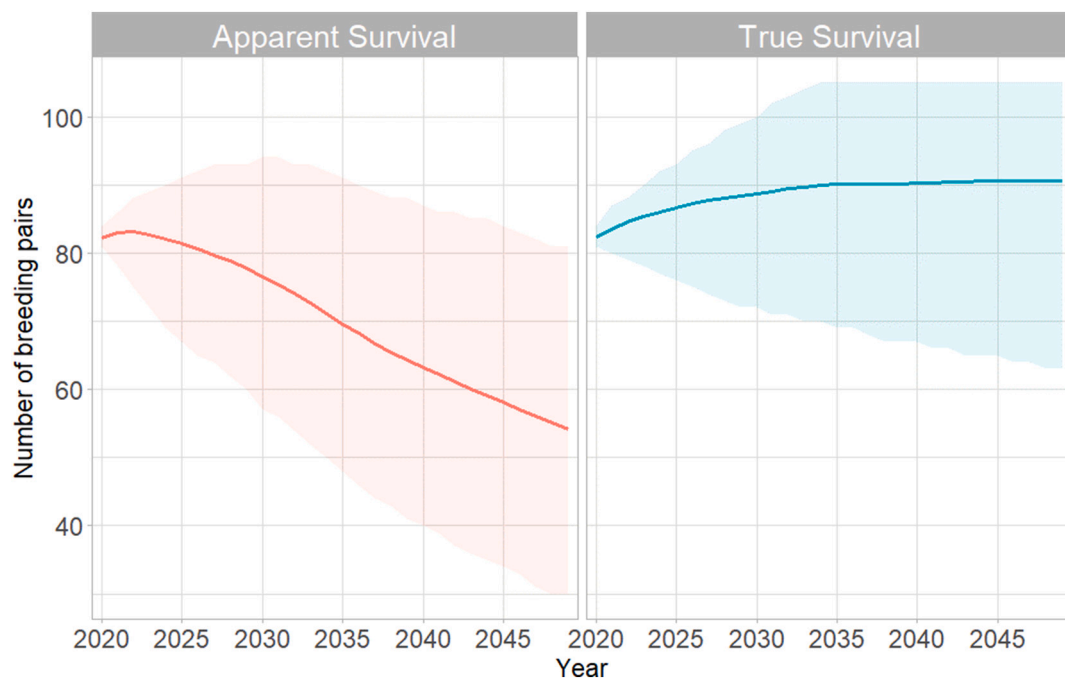


Fig. 3. Means (solid lines) and 90 %CIs (shaded areas) of the numbers of breeding pairs projected by the PVAs between 2020 and 2049 under the use of apparent and true survival.

(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.

3.4. Explicit modelling of dispersal processes - fit to observed population numbers (2008–2020)

The addition of immigration in apparent survival PVAs progressively improved the fit of PVA results to the observed number of pairs (Fig. 4). 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 overpredictions of population growth rates and population sizes (i.e., nine immigrants: $D = 0.313$).

4. 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 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 dispersal processes explicitly in

demographic PVAs.

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. Importantly, differences of such magnitude may have considerable implications for conservation and management. The use of apparent survival may justify relatively urgent management based on the perception that the population is rapidly declining, while true survival projections may lead to optimistic population status conclusions. Interestingly, differences between the true and apparent 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 predictions (Sæther and Bakke, 2000). Given the large prevalence of permanent emigration, differences of this magnitude or larger between survival types may be common across species. For instance, in passerines, Schaub and 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). Therefore, such differences may also have considerable implications for conservation and management across species.

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,

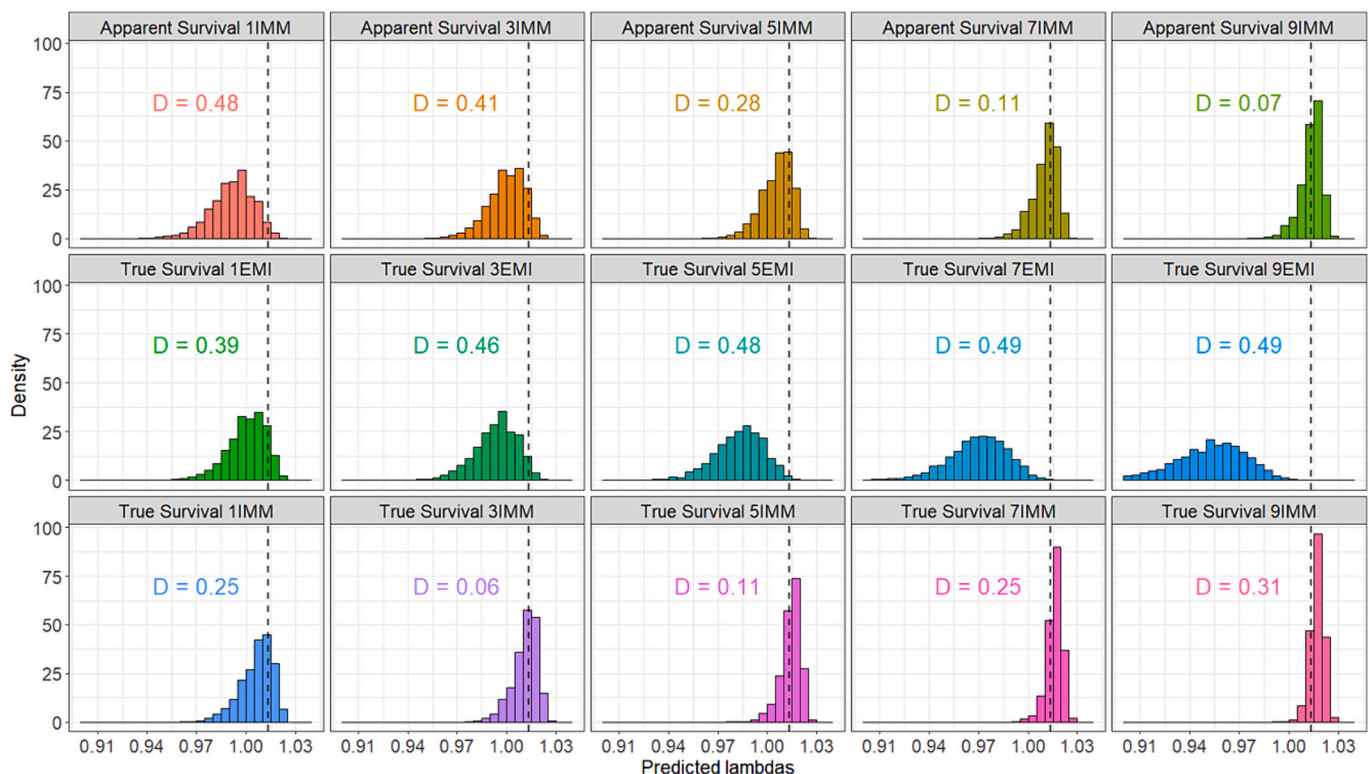


Fig. 4. Histograms showing the densities of binned predicted lambdas (binned by groups of 0.005 units) of the PVAs projected between 2008 and 2020 under the use of apparent and true survival, and the explicit modelling of emigration and immigration. Black vertical dashed lines indicate the observed lambda from census data in the study population. Predicted and observed lambdas were calculated as the geometric mean of 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 emigrants; 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.

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 and Collopy, 2013), and hence the risks of obtaining such biased PVA results may be considerable across populations and studies. Even so, PVA predictions based on apparent survival 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 (Pulliam, 1988; 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, which may be a plausible scenario for many species in the present context of wide-scale biodiversity crisis (Schaub and Ulrich, 2020). From this perspective, these “conservative” viability estimates may promote population management from a cautionary perspective.

Nevertheless, researchers and managers should consider that the use 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 could 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 al., 2007; Horton and Letcher, 2008), and 2) the dispersal capacity of the study species/population (Greenwood and Harvey, 1982; Horton and Letcher, 2008). Dispersal capacities may strongly vary among 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). From this perspective, it appears essential that the interpretation of PVA outcomes based on apparent survival, and subsequent conservation decision-making, should be undertaken considering the potential effect of permanent emigration and its main determinants.

An explanation for the relatively adequate fit of the true survival PVA to observed census data may be that 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 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 dispersal processes are not at equilibrium (Schaub et al., 2010; Mihoub et al., 2011; Furrer and Pasinelli, 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 dispersal 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 statement 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 dispersal processes are not explicitly modelled may be restricted to specific population scenarios. Thus, estimating emigration and immigration 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 allow the estimation of emigration probabilities from the combination of mark-resighting data and the locations of sightings (Schaub and Royle, 2014; Badia-Boher et al., 2023). For example, these models estimated permanent emigration at ca. 38 % in the study population (Badia-Boher et al., 2023). Another analytical tool to be considered is Integrated Population Modelling (IPMs; Schaub and Abadi, 2011). Such models have the ability of estimating immigration, or even the combination of emigration and immigration, without explicit information about them based on the indirect information contained by the different ecological datasets used, such as productivity, mark-resighting, or census data (Abadi et al., 2010; Nuijten et al., 2020; Wiegers et al., 2022). IPMs can be easily extended into the future to perform stage-structured Bayesian Population Viability Analysis incorporating such estimates of dispersal processes (Schaub and Kéry, 2022). Otherwise, migration estimates from IPMs, and their associated uncertainties could be easily incorporated into non-Bayesian PVA structures. Additionally, while in this work we focused on permanent emigration, temporary emigration can also be a frequent and important process in demographic studies and could also be incorporated by using estimates provided by adapted CMR extensions, like the Pollock's Robust Design approach or specific multistate structures (Kendall et al., 1997; Schaub et al., 2004).

Even with these improvements in the estimation of emigration and immigration, PVAs are often used in threatened species with low population sizes and substantial data limitations (e.g., scarcity, poor quality, or lack of specific data types, Beissinger and Westphal, 1998; Nicol-Harper et al., 2023), 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 dispersal 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 and Westphal, 1998; Pe'er et al., 2013). 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 and Westphal, 1998; Morris and Doak, 2002; McGowan et al., 2011). Thus, 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 dispersal 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 dispersal processes. In this sense, potential solutions may be gathering different types of ecological data (i.e., tag-resighting, productivity, counts) for their use in integrated analyses, and/or obtaining telemetry data to quantify dispersal and draw estimates on dispersal processes (Cadahía et al., 2010). Alternative solutions may include enlarging study area size to diminish the effect of dispersal processes in local population dynamics (Zimmerman et al., 2007; Horton and Letcher, 2008). In situations where these solutions cannot be implemented, model calibration may be fundamental to improve the reliability of PVA projections (Beissinger and Westphal, 1998; Pe'er et al., 2013). 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 productivity, and other key vital rates for population dynamics. Furthermore, these parameters may show complex variations across population stages like sex and age classes (Pusey, 1987; Badia-Boher et al., 2023). However, most often, PVA projections may not have enough information to predict or account for these potential variations driven by ecological determinants, 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, and conservation decision-making may be essential to maximize the benefits of PVAs as an analytical tool for conservation (Bakker and Doak, 2009). In this respect, PVAs may serve as a framework to evaluate the effectiveness of conservation actions undertaken in previous stages of conservation programmes, and to calibrate to observed data and revisit former predictions when further demographic and ecological data become available, so that future actions can be implemented considering all the quantitative knowledge gained.

CRedit authorship contribution statement

Jaume A. Badia-Boher: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Joan Real:** Data curation, Funding acquisition, Supervision, Validation, Writing – original draft, Writing – review & editing. **Antonio Hernández-Matías:** Conceptualization, Data curation, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

The code used in this study is available in the figshare repository, <https://doi.org/10.6084/m9.figshare.23107829.v2>.

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Appendix A. Supplementary data

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