**Conservation implications of a mismatch between data availability and demographic impact**

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# **Abstract**

Cost-effective use of limited conservation resources requires understanding which data can most contribute to alleviating biodiversity declines. Interventions might reasonably prioritise life-cycle transitions with the greatest influence on population dynamics, yet some contributing vital rates are particularly challenging to document; such pragmatic decision-making risks suboptimal management if less is known about influential rates. We aimed to explore whether study effort aligns with demographic impact on population growth rate, *λ*.

We parameterised a matrix population model using meta-analysis of vital rates for the common eider (*Somateria mollissima*), an increasingly threatened yet comparatively data-rich species of seaduck. Female common eiders exhibit intermittent breeding, with some established breeders skipping one or more years between breeding attempts. We accounted for this behaviour by building breeding propensity (= 0.72) into our model with a discrete and reversible ‘non-breeder’ stage (to which surviving adults transition with a probability of 0.28).

The transitions between breeding and non-breeding states had twice the influence on *λ* than fertility (summed matrix-element elasticities of 24% and 11%, respectively), whereas almost 15 times as many studies document components of fertility than breeding propensity (*n* = 103 and *n* = 7, respectively). Through comparative re-analyses, we find similar results for two amphibian species, further supporting our finding that study effort does not always occur in proportion to relative influence on *λ*. Our workflow could form part of the toolkit informing future investment of finite resources, to avoid repeated disconnects between data needs and availability thwarting evidence-driven conservation.

**Keywords**: Breeding propensity; Common eider; Matrix-element elasticity; Seaduck; Meta-analysis; Vital rate

# **Introduction**

In the face of population declines and species extinctions, biodiversity conservation functions as a crisis discipline (Soulé, 1991; Díaz *et al*., 2019). Limited resources compel conservation managers to triage their actions according to the best available data (Gerber, 2016). However, surveys of the state of conservation science have identified gaps in coverage and emphasised the important role of a ‘practice-oriented research agenda’ in meeting the information needs of practitioners (Lawler *et al*., 2006; Braunisch *et al*., 2012). Data optimisation is thus imperative, and population ecology plays a vital role in informing this process.

Mathematical population models are an essential component of the conservation toolkit (Morris & Doak, 2002; Frederiksen *et al*., 2014), but they often lack empirical estimates of the parameters needed for calibrating predictions. In a survey of mammals, birds, reptiles and amphibians, Conde *et al*. (2019) discovered a total absence of demographic data for just under 55% of the 32,144 species assessed, with a further 32% described only by summary measures. Stage-specific survival and fertility values were available for < 2%. Data deficiency thus inhibits biodiversity conservation because we lack foundational information across the life-cycle on the probability of births and deaths, with quantitative information on the uncertainty around any estimates that we do have often insufficient (but see e.g. Newton, 2010). Population modelling can increase efficiency in the face of data scarcity by directing research effort towards those vital rates that most influence projections of population dynamics (Heppell *et al*., 2000), or investment of conservation funds (Baxter *et al*., 2006).

Where they are accessible, vital rates stratified by stage (often age) inform our understanding of population dynamics (Caswell, 2001; Colchero *et al*., 2019). A common way to organise such rates is in matrix population models (MPMs), which represent (st)age-structured life histories in a mathematical format that yields emergent properties with meaningful demographic interpretations (Caswell, 2001). A key contribution of MPMs to conservation biology is perturbation analysis, which identifies each matrix element’s contribution to the asymptotic population growth rate *λ*, generating absolute sensitivities and relative elasticities (Caswell, 2001; Heppell *et al*., 2000).

These measures present an opportunity to optimise management by identifying the most responsive stage for targeted intervention. For example, a classic study on a slow life-history species, the loggerhead turtle *Caretta caretta*, found that while eggs and hatchlings received the majority of management interventions, *λ* was most influenced by juvenile survival. Egg protection alone would be insufficient to prevent eventual extinction, but population stability could be achieved with a 14% increase in juvenile survival, with turtle excluder devices a candidate solution to reduce mortality from fisheries bycatch (Crouse *et al*., 1987).

The choice of vital rates for empirical study is often decided by other priorities than their influence on demography. For instance, while adult survival will invariably be considered wherever data availability allows, breeding propensity, which describes the probability of established breeders attempting breeding in a given year, is less commonly estimated in the field, due in part to the frequent assumption that individuals will continue to attempt breeding every year after recruitment.

When breeding propensity is estimated, and found to be less than 1, it is often incorporated into MPMs simplistically, through a proportionally reduced fertility. For example, if breeding propensity were 0.75 – i.e. only three-quarters of individuals attempt breeding in any one season – fertility would be reduced by one-quarter (e.g. Etterson *et al*., 2011, Eq. (1b)). However, this can be modelled more flexibly by distinguishing breeding and non-breeding states, with breeding propensity incorporated into the transitions (e.g. Fujiwara & Caswell, 2001). This formulation provides scope to add complexity based on the distinct underlying mechanisms of attempting to breed (as measured by breeding propensity) and subsequently raising offspring (fertility).

The choice of breeding-propensity model is not merely a technical consideration. Longitudinal studies from across the animal kingdom have revealed prevalent intermittent breeding, whereby some established breeders skip one or more years between breeding attempts (e.g. Rivalan *et al*., 2005; Desprez *et al*. 2018). One such case is the common eider (*Somateria mollissima*), a widespread and abundant species of seaduck, with a long lifespan, deferred breeding, and iteroparous life history. This much-studied species presents a relatively data-rich exemplar of a slow life-history strategy (Koons *et al*., 2014). Despite its abundance, the IUCN Red List categorises the common eider as ‘Near Threatened’ globally and ‘Endangered’ in Europe, where it is projected to decline by 63% over three generations to 2033 (BirdLife International, 2018, 2021). Conservation managers thus have much to gain from understanding which of its life-history components contribute most to population change.

Here we investigated whether conservation of the common eider is currently informed by optimised demographic data collection. In order to assess whether life-stage transitions have been studied in proportion to their influence on population dynamics, we first conducted a meta-analysis of vital rate estimates, from literature review and a call for unpublished data (Nicol-Harper *et al*., 2021). Our meta-analytic estimates then allowed us to parameterise an MPM with weighted mean values to investigate which life-stage transitions most influence common eider population projections. Finally, we compared these matrix-element elasticities to their respective data availabilities, assessing our findings against the likelihoods of mismatch predicted by probability analysis. We repeated our methodology to perform re-analyses of published studies. Our workflow should therefore inform future data collection for other species, towards more efficient and informative population modelling and management.

# **Material and Methods**

## **2.1 Data synthesis**

### **2.1.1 Data collection**

This study uses the vital rate database from Nicol-Harper et al. (2021), for which data-gathering was supplemented with a call for data through the IUCN Species Survival Commission’s Duck Specialist Group. We consider this to be equivalent in purpose to requesting information from agencies with a management mandate, as advocated for meta-analyses by Beston (2011). Here we use the same vital rates as in the linked database: first-year survival (alternatively measured from hatching or fledging); second-year survival; adult annual survival; recruitment propensities; breeding propensity of established female breeders; clutch size; hatching success; and fledging success. We facilitated screening of studies and estimates by assessing verification status (whether we found the estimate in its original source, or only a citation thereof); precision (whether the estimate presented was a point estimate or simply the midpoint of an observed range); and independence (in relation to multiple estimates provided by the same study, or separate studies based on the same datasets). Verification and precision were subject to sensitivity analyses (see below and Appendix A), while decisions and results relating to independence are described below and illustrated with an example in Appendix B. We focus on female-female transition rates for analytical tractability (Caswell, 2001); see section 2.2.1.

### **2.1.2 Meta-analysis**

We did not apply formal meta-analysis to vital rates with < 20 independent estimates, which also lacked sample sizes for > 1/3 of the independent estimates; instead, for these we calculated simple means. For the vital rates undergoing formal meta-analysis, we first checked whether means were sensitive to inclusion of unverified estimates or estimates based on range midpoints. Such sensitivity analysis, as recommended by Lajeunesse (2010) for cases where selected subsets of data may lead to different ‘pooled conclusions’, revealed that inclusion of unverified estimates, or those based on range midpoints, did not significantly alter mean estimates (see Appendix A). We therefore retained these estimates for completeness, in line with Beston’s (2011) meta-analytic approach to include third-party data where original sources are unavailable due to language or access restrictions.

Where a study presented multiple estimates for one vital rate, we either (*i*) conducted a sub-meta-analysis across spatiotemporal replicates within a study (following a similar protocol to our main meta-analyses), or, if this was inappropriate or not possible, (*ii*) selected the most appropriate for our purpose (e.g. the most precise, with justification provided in the database metadata). Our use of the term ‘sub-meta-analysis’ differs from that of Zoogman *et al*. (2015), but our decisions align with the suggestions of Mengersen *et al*. (2013 [Situation 1 in Table 16.1]) and Haddaway *et al*. (2020 [Problem 7 - mitigation]) for maintaining independence among heterogeneous samples.In all cases, the aim was to ensure that meta-estimates were calculated on independent replicate observations. All inclusion decisions are described within the database metadata and/or our provided code.

Variance estimates were included when available or calculable, to inform precision-weighting (see below and Borenstein *et al*., 2009). For survival estimates based on mark-recapture modelling – such as using Program MARK (White & Burnham, 1999) – the standard error outputted from the programme was squared to obtain the variance for the populations from which the sample was drawn.

Our meta-analyses used a random effects error structure, to allow for likely variation in population means across the geographic range of the common eider (Frederiksen *et al*., 2005; Guéry et al., 2017). We followed protocols in Doncaster and Spake (2018) for mean-adjusted precision weighting, which removes a bias in meta-estimation caused by inclusion of studies with little replication. This method also allows precision-weighting of studies that provide replication but no variance estimate, on the assumption that the average of available variances applies to all studies (see Doncaster & Spake, 2018). The mean adjustment uses *s*2, the mean of study-level variances s*i*2, to calculate an error variance for each study *i*:

*vi* = *s*2 / *ni*,

where *ni* is the sample size of study *i*. The study-level error variance *vi* informs the precision weighting of each study-level mean δ*i*, with lower *vi* expressing higher precision. For a random effect, the appropriate precision weighting is:

*Wi* = 1/(*vi* + *T*2),

where *T*2 is the estimate of between-study variance. For a one-sample mean, we obtain an unbiased estimate of *T*2 from Cochran’s τ2 estimator (see ‘Hedges and Olkin method’ in Veroniki *et al*., 2016):

*T*2 = var(δ*i*) – mean(*vi*).

Finally, the standard one-sample meta-estimation by the mean of weighted means equals:

(Σ *Wi* δ*i*)/Σ *Wi*,

with associated meta-variance equal to 1/Σ *Wi*. Studies thereby contribute to the meta-estimate and meta-variance in unbiased proportion to their precision (see Doncaster and Spake, 2018). Appendix B shows a worked example across a subset of the adult survival dataset.

## **2.2 Modelling**

### **2.2.1 Life-cycle formulation and matrix population model**

Seaducks are modelled as birth-pulse populations, because they have a defined breeding season within the annual cycle (Caswell, 2001; Morris & Doak, 2002). Population projections must consequently choose to start the annual cycle either pre- or post-breeding. We used a pre-breeding life-cycle, in recognition of the complications that can arise from post-breeding formulations (Kendall *et al*., 2019). The life-cycle diagram and MPM thus project individuals from just before laying in year *t* to just before laying in year *t*+1. This means that the youngest individuals at the start of the time-step are just less than a full year old, referred to as 1-year-olds. Following projection, they will be just short of two years old, and therefore physiologically capable of breeding that season.

We restricted our models to females, because the vast majority of survival estimates are based on nesting birds (eiders are uniparental incubators; Waltho & Coulson, 2015). Male-only and aggregated survival estimates were therefore not carried over from the database (*n* = 14 estimates across 8 studies). As females are the limiting sex in ducks, which have male-biased adult sex ratios, they will generally drive *λ* (Baldassarre & Bolen, 2006). We halved the fertility estimate to account for an approximately equal sex ratio at hatching (Lehikoinen *et al*., 2008).

Our model partitions ‘pre-breeder’ into ages of 1 (sexually immature) to 4 years old (final year for recruitment deferral), making use of available age-stratified recruitment data. Recruitment probabilities were based on (*i*) estimates of breeding propensity at 2 years old, 3 years old (including repeat breeders) etc.; and (*ii*) estimates of proportion of recruits first breeding at each age (which must sum to 1 across all ages). For the purposes of our model, we needed the former, but could improve our estimates by incorporating the latter (see Appendix C).

Intermittent breeding has previously been represented in life-cycles through proportionally reduced fertility, including for seaducks (e.g. Flint *et al*., 2016; Koneff *et al*., 2017; Tjørnløv *et al*., 2019). For the common eider, mean adult female breeding propensity has been estimated as 0.72 (Nicol-Harper *et al*., 2021). We incorporated a discrete and reversible ‘non-breeder’ stage, to which surviving individuals not attempting breeding transition, as determined by breeding propensity: p(non-breeding) = 1 - 0.72 = 0.28. Surviving adults can therefore transition: from breeder to breeder (‘continued breeding’) or non-breeder to breeder, both with probability 0.72, or from non-breeder to non-breeder (‘continued non-breeding’) or breeder to non-breeder, both with probability 0.28. In the absence of disaggregated survival estimates for non-breeding and breeding states, we assume these transitions to be underlaid by the same survival probability. Infertility would be accounted for within fertility estimates (e.g. clutch size or hatching success = 0) rather than breeding propensity (infertile females could attempt breeding).

In the MPM itself (Fig. 1), each matrix entry *aij* represents the contribution of individuals in the *j*th stage (column) of year *t* to the *i*th stage (row) of year *t*+1. All transitions are subject to survival: individuals alive in year *t* must survive in order to occupy a stage in year *t*+1. A 1-year-old, assuming it survives, transitions either to the breeder stage or to the 2-year-old pre-breeder stage. An individual surviving to 5 years old must transition to the breeder stage, as this is the oldest observed age of recruitment. Breeders contribute 1-year-olds to the following year’s population, provided that the eggs laid hatch successfully, the hatchlings fledge successfully, and the fledglings survive until the following year (with the final two transitions being measured either separately or in combination, as s1f and FS, or s1h, respectively). Once an individual has bred, it can transition between breeder and non-breeder each subsequent year, or remain in each stage for any number of years, given survival.

### **2.2.2 Perturbation analysis and comparison with study effort**

We obtained matrix-element elasticities, the proportional contributions to *λ*, from the elas() function of the R package *popdemo* v1.3-0 (Stott et al., 2018). For comparative purposes, we group elasticities based on transition types: (i) ‘Recruitment’ for transitions to breeding for 1- to 4-year-olds; (ii) ‘Breeding transitions’ including continued breeding, continued non-breeding, breeder to non-breeder, and non-breeder to breeder; and (iii) ‘Reproduction’ for fertility i.e. breeder to 1-year-olds. The corresponding study effort on each of these three transition types was calculated as the number of contributing studies divided by the total number of studies across all vital rates. With many studies contributing to more than one of the three transition types, the three study-effort fractions may not sum to one.

For each elasticity, we calculated the deviation of its corresponding fractional study effort from an exact match. We then measured the probability of this deviation occurring by chance. For example, an elasticity of 0.3 might have a corresponding fractional study effort of 0.6, which then has a probability of 0.4 (= 1 – 0.6) of chance over-representation by at least this; or an elasticity of 0.6 might have a corresponding fractional study effort of 0.3, which then has a probability of 0.3 of chance under-representation by at least this.

We further considered the generality of our results through comparative re-analyses, applying our elasticity-study effort comparison workflow to published demographic meta-analyses for amphibians (Western toad, *Bufo boreas*, and long-toed salamander, *Ambystoma macrodactylum*; Vonesh & de la Cruz, 2002), spotted owl (*Strix occidentalis*; Boyce *et al*., 2005), and black bear (*Ursus americanus*; Beston, 2011). In each case, elasticities were calculated or extracted, and compared to the study effort involved in parameterising the relevant vital rates/matrix transitions. For details see Appendix D and associated R code.

### **2.2.3 Software and data**

Data handling and analysis was implemented in R software v4.0.3 (R Core Team, 2020). Packages were used to handle data (*tidyr* v1.1.4, Wickham, 2021) and generate figures (*metafor* v2.4-0, Viechtbauer, 2010; *RColorBrewer* v1.1.2, Neuwirth, 2014; *forestplot* v1.10.1, Gordon & Lumley, 2020; *fields* v.13.3, Nychka *et al*., 2021). The underlying database is available from the Dryad Digital Repository [<https://doi.org/10.5061/dryad.x3ffbg7ks>] (data paper: Nicol-Harper *et al*., 2021); R code and input files for this study are deposited on Figshare (see Data Availability Statement).

# **Results**

## **3.1 Data availability**

Of the 134 studies in the database, 129 were used here. The five unused studies are flagged in the original database as not contributing any vital rates (rather, acting as verified sources for unverified estimates). The numbers of studies and estimates varied greatly among the parameters, with some parameters having multiple estimates per study across years or locations (Table 1). Of the seven studies estimating breeding propensity at 2 years old, a subset of six also estimated breeding propensity at 3, of which two also estimated breeding propensity at 4 and 5. Clutch size, hatch success, fledging success, and first-year survival (from hatching or fledging) all contributed to fertility estimates, with 103 unique studies between them.

## **3.2 Mean vital rate estimates**

We had sufficient estimates (and associated sample sizes) to calculate weighted means for adult survival, clutch size, and hatching success; the other vital rates are estimated with a simple mean only (Table 1). The mean estimates for second-year and adult survival were very similar, and while few individuals recruit at the earliest possible age of 2 years old, by 4 years old breeding propensity is very similar to that of recruited individuals. For forest plots and funnel plots representing the meta-analyses, see Appendix E.

## **3.3 Parameterised life cycle**

The parameterised life-cycle shows transitions between stages as calculated from the mean vital rate estimates (Fig. 2). The associated *λ* was 0.99 (to two decimal places), representing an expectation of 1% decline per year for a stable stage structure.

## **3.4 Elasticities**

Transitions between breeding and non-breeding states (elasticities summing to 24%) had an influence on *λ* that was secondary only to continued breeding (38%), and a much greater influence than fertility (11%, Fig. 3).

## **3.5 Comparison of data availability and elasticities**

We compared the study-effort fractions for each grouped transition with their respective contributions to *λ* (summed matrix-element elasticities). The grouped transitions can be matched to the matrix element elasticities in Fig. 3 as follows: ‘Reproduction’ represents fertility (in the top row), ‘Breeding transitions’ represent the four transitions in the bottom-right, and ‘Recruitment’ represents the remaining transitions (i.e. those left of the breeder column). The paired fractions in Fig. 4 show that: recruitment has been studied approximately in proportion to its importance in predicting population dynamics; reproduction is overrepresented (largely due to clutch size; see Table 1); breeding transitions are underrepresented.

This case study of the common eider uncovers a mismatch for this species specifically, but probability analysis shows that disparities will still tend to occur even with more equally distributed elasticities (contours in Fig. 4). This is because a random distribution of fractions summing to 1 (e.g. matrix-element elasticities) more frequently has one high fraction, forcing the others low, than it has one low and several high, and it cannot have several very high fractions. In consequence, disproportionately high study effort will likely be associated with vital rates of low relative importance unless purposefully aligned with importance. Hence, gathering data on those vital rates that are easiest to determine will be unlikely by chance alone to cover those with highest demographic importance.

Our comparative re-analyses covered a range of possible mismatch scenarios. The two species of amphibian generated similar plots to the common eider, with adult survival relatively understudied and fertility relatively over-studied (Appendix D Fig. D.1). The spotted owl represented the special case where (almost) all studies contribute to all transitions, with the study being based on a research programme where each of the three vital rates of interest was recorded at almost all of the sites considered. For the black bear, the elasticity-study effort combinations generated a plot where all transitions appear over-studied, although once again early-life vital rates are overrepresented relative to adult survival (Appendix D Fig. D.2).

# **Discussion**

We have used data synthesis and matrix population modelling to reveal a mismatch across life-stage transitions between data availability and potential influence on population dynamics, in a data-rich species of increasing conservation concern. Specifically, for the common eider, transitions between breeding and non-breeding are strongly influential on *λ*, and their component vital rates are understudied relative to fertilities.

The abundance of data on reproduction, and particularly clutch size, is unsurprising for this study species. Nesting female eiders are colonial, site-faithful, constant incubators, and amenable to close observation, even tolerating being lifted off the nest by hand in some cases (Afton & Paulus, 1992; Waltho & Coulson, 2015). The common eider is a charismatic species, whose reproduction is monitored by researchers, subsistence egg collectors and commercial eiderdown farmers (Cooch, 1986; Jónsson *et al*., 2009). The number of eggs per nest is straightforward to record on a single visit, although nesting-season phenology may need to be considered to account for incomplete and partially predated clutches (Paynter, 1951; Sénéchal et al., 2010).

In contrast to fertility, transitions between breeding and non-breeding states are determined by survival and breeding propensity, which can only be estimated with in-depth studies involving multiple visits, re-sighting and/or recovery of individuals. Our mean estimate of adult survival seems fairly low compared to other comparative analyses (Waltho & Coulson, 2015; Koneff *et al*., 2017); this may be at least partially due to the fact that many estimates relate to apparent rather than true survival, and therefore do not account for the possibility of emigration.

Assessments of the role that demographic parameters such as breeding propensity play in population dynamics and hence viability are contingent upon having robust, unbiased datasets. Any uncertainties in the identity of each breeding female in any given year will confound estimates of breeding propensity in ways that cannot readily be captured by confidence intervals. For example, an individual that reappears after a year of absence may have skipped breeding or may have bred without being recorded in nest surveys (Coulson, 2010). A potential solution is the use of dataloggers or telemetry devices. For example, if a breeding female were equipped with a datalogger in year *t*, but not found in year *t*+1, then subsequent retrieval of the datalogger could suggest incubation in year *t*+1 with a detected a sustained decrease in light levels, or non-breeding if the season was spent primarily on water (C. Mitchell, pers. comms., 2019). Similarly, the activity patterns of individuals fitted with telemetry devices can indicate whether or not a breeding attempt was made (Weegman *et al*., 2017).

Our mean vital rate estimates, and therefore our parameterised life-cycle, can represent only what is presented in the database, which potentially deviates from any true stable state. Firstly, we suspect that many studies assume a breeding propensity of 1 by default (e.g. Kats, 2007). While this could approximate reality for some subpopulations, if breeding propensity has not been measured then we have no way of assessing that assumption. It follows that untested assumptions of consecutive breeding may mask significantly lower population growth rates. Additionally, λ refers to steady state dynamics, whereas the populations providing vital rate and population trend estimates are likely subject to transient effects due to disturbance.

## **4.1 Wider implications**

Our comparative re-analyses of published vital rate meta-analyses provide evidence for mismatches in other vertebrate species, with two species of amphibian (Western toadandlong-toed salamander) similarly exhibiting relative understudy for adult survival and relative overstudy for adult fertility. In the case of the black bear, where all transitions appear to be ‘overstudied’, the management recommendation might be for studies that are not able to estimate all parameters to prioritise sub/adult survival (with smallest deviances from optimal) at the expense of fecundity and cub survival (with largest deviances from optimal). The comparative re-analyses also demonstrate how our workflow can be replicated in other systems, allowing a more effective use of limited resources to build the most instructive evidence base. Without strategies considering optimal effort distributions where studies cannot estimate all vital rates, data gatherers will tend to over-study the parameters that contribute least, and under-study those that matter most.

In many cases, a principal driver of such mismatches may be the relative ease of collecting data from certain life-stages rather than those of most immediate relevance to conservation interventions, as with the accessible hatchlings versus elusive juvenile loggerhead turtles (Crouse *et al*., 1987). We highlight breeding propensity as a vital rate which is often completely overlooked, even by those attempting to focus on the most important variables. Of the seven studies estimating breeding propensity, four studies estimate at least two (and in one case, seven) further vital rates, demonstrating that breeding propensity is not necessarily an overly ambitious addition to existing data-gathering programmes focussing on other vital rates. More generally, for species for which we have little or no demographic data (Conde *et al*., 2019), we can still make informed judgements about what is *likely* to be most important, by considering better-studied proxy species.

In contrast, well-studied rates provide the opportunity to investigate the role of inter-population variation across geographic ranges and different environments (Frederiksen *et al*., 2005). In the case of the common eider, we found little evidence for systematic variation in vital rates across subspecies or candidate environmental explanatory variables (data not shown), so are comfortable with the use of a species-wide life-cycle parameterisation. In cases where there is more significant intraspecific variation, the workflow used here might need to be conducted separately for a number of subpopulations.

We are conscious that the available data for this study is less than all the collected data. There will be other unpublished datasets, as well as data published in languages and sources inaccessible for this study. We don’t wish to suggest that data-gatherers should stop collecting more easily recorded data such as egg counts, because more data improves precision and accuracy of estimates, and facilitates estimation of regional variation. Furthermore, in some cases study effort may need to be directed towards those vital rates which are most variable, in order to better parameterise the envelope of expected values.

We also acknowledge that vital rates are usually estimated as part of data-gathering exercises to answer specific study questions, hence not necessarily with the full life-cycle in mind. Conservation policymakers and practitioners are often making best use of the data available to them, which was often collected opportunistically as part of other activities (Dobson *et al*., 2020). Nevertheless, if our aim is to reduce uncertainty in population projections, then the available data on common eider have a suboptimal distribution across parts of the life-cycle. The more-the-better maxim does not negate the fact that not all data are equally useful; in some cases, the most useful data will be those necessitating a redirection of effort from vital rates which are easier to measure but less informative, in favour of more targeted application. Canessa *et al*. (2015)demonstrate how ‘value of information’ analysis can be used to determine the expected benefits of investment in obtaining further information, including in a demographic context.

While return on investment should be at the core of each funding body’s ethos, conservation is not a top-down enterprise; strategic decisions, and funding thereof, tend to be made at the level of individual organisations, rather than across all agencies collectively managing data-gathering for a particular species. Nevertheless, there are examples of a more strategic approach: of particular relevance to the common eider is the Sea Duck Joint Venture, which publicised a “strategic shift in focus” towards a programme “intended to provide information most needed by managers to make informed decisions” (SDJV Management Board, 2014, p. 4). Similarly, multi-national species conservation action plans, such as those produced by the African-Eurasian Waterbird Agreement, provide a means of highlighting the relative value of demographic data to researchers, which could help to direct research efforts towards the data most needed to inform conservation assessments. More generally, the British Trust for Ornithology is already very successful in directly enthusing citizen scientists to collect specific types of data.

Strategic projects nevertheless require long-term resourcing to ensure sustainable collection and maintenance of the valuable individual-based longitudinal datasets required to parameterise full life-cycles of long-lived species (Culina *et al*., 2020). The focus here is on asymptotic population growth rate as the conservation target, but such datasets support a range of outputs, not least the vital rate estimates themselves. Additionally, adoption of MPM-derived priorities may necessitate greater engagement by population ecologists, in demonstrating the utility of population models and exactly what data are required for them. Green (1995) and Frederiksen *et al*. (2014) highlight the fundamental role of population models in species recovery, and make a strong case for collaboration between biologists modelling population declines, and conservationists making action plans to reverse them.

In conclusion, our results highlight a propensity for disconnects between empirical demographic data and the information needs of conservation biologists and wildlife managers. Where perturbation analysis is used to inform investments into future conservation research and interventions, it will be important to minimise such mismatches by aligning study effort with demographic importance where practicable. There would be great value in enhanced collaboration and co-ordination between citizen scientists, ecologists and population modellers to co-produce the knowledge around the difficult-to-measure rates that are needed to successfully and effectively manage taxa of conservation concern.

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# **Tables**

Table 1. Number of studies and independent estimates per vital rate across our database, and estimated mean values as used in our analysis. For the meta-analysed vital rates (sa, CS and HS), the number of independent estimates informing the estimated mean refers to the number of estimates used in the meta-analysis, which excludes estimates without sample sizes, and combines some estimates through sub-meta-analysis. Abbreviations as for Fig. 1; FB = first breeding (i.e. recruitment propensity at age *x*), FS = fledging success. Estimated means rounded to two decimal places; variances rounded to one significant figure.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Vital rate** | **Number of studies** | **Number of independent estimates informing estimated mean** | **Estimated mean** | **Variance** | **Calculation method** |
| **s1h** | 3 | 3 | 0.37 | 0.08 | Simple mean |
| **s1f** | 3 | 3 | 0.75 | 0.02 | Simple mean |
| **s2** | 7 | 7 | 0.87 | 0.008 | Simple mean |
| **sa** | 35 | 15 | 0.86 | 0.0003 | Meta-analysis |
| **FB** | 7 | 7 | *x* = 2: 0.17  *x* = 3: 0.58  *x* = 4: 0.71  *x* = 5: 1 | N/A due to underlying calculations | As described in 2.2.1 |
| **BPeb** | 7 | 6 | 0.72 | 0.03 | Simple mean |
| **CS** | 91 | 66 | 4.08 | 0.004 | Meta-analysis |
| **HS** | 27 | 11 | 0.61 | 0.005 | Meta-analysis |
| **FS** | 13 | 13 | 0.22 | 0.01 | Simple mean |

# **Figure legends**

Figure 1. Matrix population model based on our life-cycle formulation for the common eider. Blank entries represent impossible transitions. Abbreviations: 1yo = 1-year-old; PBx = x-year-old pre-breeder (e.g. PB2 = 2-year-old pre-breeder); B = breeder; NB = non-breeder; s1h = first-year survival from hatching (either measured directly, or the product of fledging success and first-year survival from fledging); s2 = second-year survival; sa = adult annual survival; BPx = breeding (recruitment) propensity at age x; BPeb = breeding propensity of established breeders; CS = clutch size; HS = hatching success. BP5 is equal to 1, as all individuals recruit by 5 years old.

Figure 2. Parameterised life-cycle for the common eider, as used in our analysis. Arrows show life-stage transitions, with stage transition probabilities displayed to two decimal places. Abbreviations as for Fig. 1.

Figure 3. Elasticity matrix, with matrix-element elasticities shown to 2 decimal places where > 0.05. Abbreviations as for Fig. 1; Elast. = elasticity. Presentation based on code developed by Steve Ellner and Dylan Childs, available at <https://github.com/ipmbook/first-edition/blob/master/Rcode/utilities/MatrixImage.R>.

Figure 4. Cross-plot illustrating study-effort fractions against relative importance as measured by matrix-element elasticities, across grouped common eider life-cycle transitions. For study-effort numerators, we counted 39 ‘Recruitment’ studies, 38 ‘Breeding transition’ studies, and 103 ‘Reproduction’ studies; in each case the denominator counts the total of 129 studies across all vital rates. The 1:1 diagonal represents the optimal proportion of studies that would cover each life-history transition if proportional to importance. Shading and contours represent the probability of a random set having at least as great a deviation from optimal at each level of importance. For example, a very low relative importance has a high probability of being overrepresented (falling above the 1:1 diagonal), and a high relative importance has a high probability of being under-represented (falling below the 1:1 diagonal).

# **Data Availability Statement**

Underlying data and code are available on Figshare:

input files: <https://doi.org/10.6084/m9.figshare.16832686>;

output code: <https://doi.org/10.6084/m9.figshare.16832878>;

comparative code: <https://doi.org/10.6084/m9.figshare.16832884>.

# **Competing Interests Statement**

The authors declare no competing interests.

# **Author Contributions**

ANH = Conceptualisation (equal), data curation (lead), formal analysis (lead), methodology (equal), software (lead), writing – original (lead), writing – review & editing (equal)

CPD = Methodology (equal), supervision (equal), writing – review & editing (equal)

GMH = Supervision (equal), writing – review & editing (equal)

KAW = Supervision (equal), writing – review & editing (equal)

THGE = Conceptualisation (equal), supervision (equal), writing – review & editing (equal)

# **Acknowledgements**

Funding: This work was supported by a UK Natural Environmental Research Council SPITFIRE DTP award [grant number NE/L002531/1] to ANH. The authors thank all respondents to the call for data, particularly Heather Major & Tony Diamond, Aevar Petersen, and Grigori Tertitski, who contributed previously unavailable data (Nicol-Harper *et al*., 2021). We also thank R. Spake for advice on our meta-analysis methodology. ANH gratefully recognises the organisers and participants of the NERC Advanced Training Short Course on stage-based demography held in January 2019, whose feedback contributed to development of this model. ANH also thanks the British Ornithologists’ Union for a Member Travel Award which supported attendance to the European Ornithologists’ Union Conference in August 2019, where an earlier iteration of this model was presented. Author contributions: ANH & THGE conceived the idea; ANH collated and analysed the data, with guidance from CPD on meta-analysis and effort-importance probabilities; ANH wrote the manuscript, with all authors contributing to drafts, and giving final approval for publication.

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# **Appendix A: Sensitivity analysis on inclusion of unverified estimates and estimates based on range midpoints**

We analysed the sensitivity of vital rate estimate means to inclusion of unverified estimates, and those based on range midpoints, using Wilcoxon rank sum tests with continuity correction (Table A.1). These are the non-parametric version of t-tests, since visual inspection of histograms, and *p*-values < 0.05 in Shapiro-Wilk tests, suggested rejection of normal distributions for the estimates of each vital rate (Table A.1). The tests were run on the full dataset as taken from the database, i.e., including non-independent estimates, and prior to sub-meta-analyses. The Wilcoxon tests compared the full dataset to a subset excluding unverified or midpoint estimates, respectively.

Shapiro-Wilk test: p < 0.05 🡪 not normally distributed.

Wilcoxon test: p > 0.05 🡪 not significantly different.

Table A.1. Outputs from Shapiro-Wilk and Wilcoxon tests on adult survival, clutch size, and hatching success.

|  |  |  |  |
| --- | --- | --- | --- |
| **Vital rate** | **Shapiro-Wilk test** | **Wilcoxon test –**  **unverified estimates** | **Wilcoxon test –**  **range midpoints** |
| **Adult survival** | *W* = 0.81176;  *p*-value = 0.0000004563 | *W* = 1345.5;  *p*-value = 0.7488 | *W* = 1599.5;  *p*-value = 0.8544 |
| **Clutch size** | *W* = 0.97845;  *p*-value = 0.0002124 | *W* = 35161;  *p*-value = 0.9346 | *W* = 42091;  *p*-value = 0.9244 |
| **Hatching success** | *W* = 0.95294;  *p*-value = 0.03107 | *W* = 1261.5;  *p*-value = 0.8706 | *W* = 1390;  *p*-value = 0.8055 |

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# **Appendix B: Example meta-analysis**

Here we work through the meta-analysis process for adult survival, starting with the sub-meta-analysis conducted on two studies, and then describing the overall meta-analysis process for the resulting set of comparable estimates. See section 2.1.2 for further detail and citations regarding justification of these methods.

For adult survival, two studies provided multiple estimates requiring sub-meta-analysis: ID’s 90 (Wood *et al*., 2021) and 91 (Ekroos *et al*., 2012). A simplified extract from the input file (based on the vital rate database in Nicol-Harper *et al*., 2021) shows that they both provide multiple estimates, standard errors, and sample sizes, across colonies and island cover types, respectively (Table B.1). Note that selecting, for example, a single estimate per study based on maximal precision (i.e. lowest provided standard error) or replication (i.e. largest sample size) would send forward to the main meta-analysis higher estimates than taking a mean (whether weighted or unweighted).

Table B.1. Simplified extract from the adult survival input file, showing studies to undergo sub-meta-analysis. SE.prov = provided standard error; n = sample size; rm\_ind.justification explains why the estimates for each study should undergo sub-meta-analysis.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| ID | Estimate | SE.prov | n | Comments | rm\_ind. justification |
| 90 | 0.94 | 0.015 | 1192 | Akureyri | for weighted mean across different colonies |
| 90 | 0.887 | 0.027 | 821 | Flatey | for weighted mean across different colonies |
| 90 | 0.922 | 0.017 | 1005 | Rif | for weighted mean across different colonies |
| 91 | 0.679 | 0.027 | 566 | forested | for weighted mean across island types |
| 91 | 0.761 | 0.013 | 566 | open | for weighted mean across island types |

Here we show the calculations involved in the sub-meta-analysis for Wood *et al*., (2021):

Step 1. Convert standard errors to variances [variance = (SE × √sample size)2]:

(0.015 × √1192)2 = 0.268200

(0.027 × √821)2 = 0.598509

(0.017 × √1005)2 = 0.290445

This step would be skipped if variances were provided by the studies, or if standard errors based on survival estimates from mark-recapture modelling had already been converted to variances as described in section 2.1.2.

Step 2. Calculate mean variance:

(0.268200 + 0.598509 + 0.290445)/3 = 0.385718

Step 3. Calculate study-level error variances, *vi*’s, as shown in main text section 2.1.2:

0.385718/1192 = 0.0003235889

0.385718/821 = 0.0004698149

0.385718/1005 = 0.000383799

Step 4. Calculate weightings, *Wi*’s, as shown in main text section 2.1.2:

Var(0.94, 0.887, 0.922) = 0.0007263333

Mean(0.0003235889, 0.0004698149, 0.000383799) = 0.0003924009

*T*2 = 0.0007263333 - 0.0003924009 = 0.0003339324

1/(0.0003235889 + 0.0003339324) = 1520.863

1/(0.0004698149 + 0.0003339324) = 1244.172

1/(0.000383799 + 0.0003339324) = 1393.279

Step 5. Calculate the meta-estimate and meta-variance, as shown in main text section 2.1.2:

1520.863 + 1244.172 + 1393.279 = 4158.314

1520.863 × 0.94 + 1244.172 × 0.887 + 1393.279 × 0.922)/ 4158.314 = 0.9181113

1/4158.314 = 0.0002404821

Step 6. Meta-variance is then multiplied by the number of contributing estimates, for compatibility with calculated variance from studies without sub-meta-analysis within the main meta-analysis:

0.0002228807 × 3 = 0.0007214463.

i.e. across the three estimates [0.887, 0.922, 0.94] in Wood *et al*. (2021), the weighted mean adult survival is 0.918 (to three significant figures) with a meta-variance of 0.0002 and associated study-level variance of 0.0007 (both to one significant figure). This is equivalent to 0.922 ± 0.03 SD (to three significant figures). The mean value is higher than when calculating a simple mean (0.916 ± 0.03 SD), because the two higher estimates are associated with greater precision. The equivalent process with the two estimates from Ekroos *et al*. (2012) generates: meta-estimate = 0.72, meta-variance = 0.002, study-level variance = 0.003, SD = 0.06.

These two estimates generated by sub-meta-analyses can then be handled equivalently to single estimates from other studies (often representing means where disaggregated data were not provided). Following removal of estimates without associated sample sizes, the adult survival dataset for meta-analysis is as shown in Table B.2.

Table B.2. Simplified extract from the adult survival dataset, following sub-meta-analyses and removal of estimates without associated sample sizes. Var.prov = provided variance; Var.calc = calculated variance; SD = standard deviation; other variables as in Table B.1.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ID | Estimate | Var.prov | Var.calc | SD.prov | SE.prov | n |
| 2 | 0.9616 | NA | NA | NA | NA | 6000 |
| 5 | 0.981 | NA | 0.000004 | NA | 0.002 | 2238 |
| 17 | 0.51 | NA | NA | NA | 0.0011 | 1166 |
| 38 | 0.805 | NA | NA | NA | NA | 163 |
| 66 | 0.882 | NA | NA | NA | NA | 6393 |
| 67 | 0.77 | NA | NA | NA | NA | 650 |
| 70 | 0.892 | NA | 0.000484 | NA | 0.022 | 361 |
| 71 | 0.826 | NA | NA | 0.099 | NA | 1118 |
| 72 | 0.85 | NA | NA | NA | NA | 862 |
| 74 | 0.9 | NA | 0.0001 | NA | 0.01 | 2340 |
| 76 | 0.827 | NA | NA | 0.023 | NA | 3028 |
| 77 | 0.89 | NA | NA | NA | NA | 150 |
| 92 | 0.89 | NA | 0.0001 | NA | 0.01 | 398 |
| 97 | 0.9 | NA | NA | NA | NA | 22320 |
| 120 | 0.824 | NA | 0.000676 | NA | 0.026 | 6500 |
| 90 | 0.918111 | NA | 0.000721 | NA | NA | 3018 |
| 91 | 0.72 | NA | 0.003362 | NA | NA | 1132 |

The meta-variances calculated from the sub-meta-analyses have become ‘calculated variances’, which are later further populated by conversion from provided standard deviations/errors from other studies where available. Beforehand, in this case two outliers are removed upon inspection: 0.51 (ID 17) as it is > 2 standard deviations below the mean value, and 0.981 (ID 5) as it substantially exceeds confidence limit bounds in the funnel plot (Figure B.1).

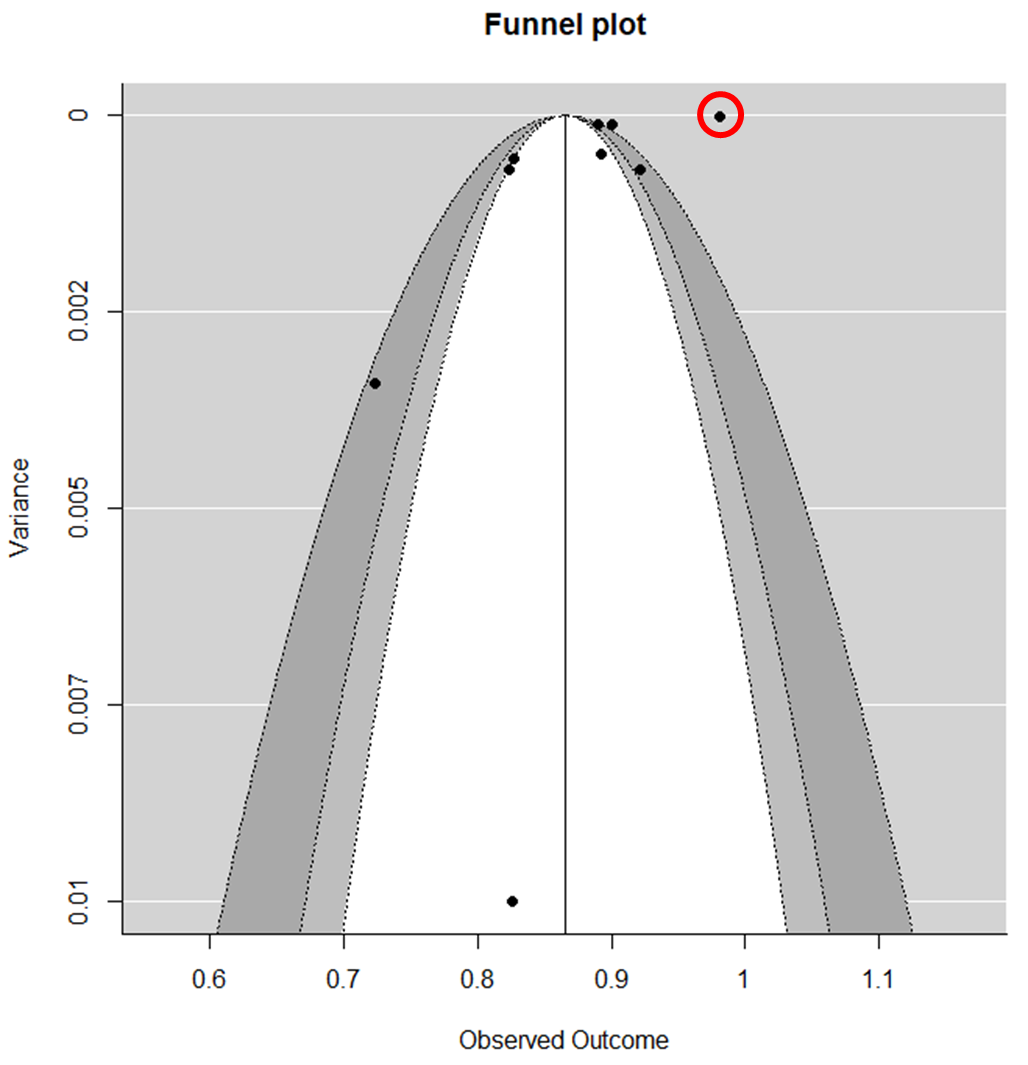


Figure B.1. Funnel plot for adult survival estimates, following sub-meta-analysis, removal of estimates without associated sample sizes, and removal of one outlier (estimate = 0.51). The remaining outlier, well outside the bounds of the 99% confidence interval, is circled in red.

The mean calculated variance across all available values (including converted from SD/SEs) = 0.001971681, and the overall weighted mean adult survival = 0.857 ± 0.0003 variance or 0.02 SD. Sensitivity analysis (code not provided) showed that adult survival would remain 0.857 to three decimal places if simple means rather than weighted means were applied to the ‘sub-meta-analysis’ studies, or even if taking a simple mean rather than applying Doncaster & Spake’s (2018) methodology across the meta-analysis dataset, with simple means applied at the study level also. The overall value would, however, be 0.861 if the most precise estimates from Wood *et al*. (2021) and Ekroos *et al*. (2012) were sent forward in place of a mean across their replicates.

For the full method, and the equivalent process for clutch size and hatching success, see provided code.

**Literature cited:**

Doncaster, C. P., & Spake, R. (2018). Correction for bias in meta-analysis of little-replicated studies. *Methods in Ecology and Evolution, 9*(3), 634–644. <https://doi.org/10.1111/2041-210X.12927>

Ekroos, J., Öst, M., Karell, P., Jaatinen, K., & Kilpi, M. (2012). Philopatric predisposition to

predation-induced ecological traps: habitat-dependent mortality of breeding eiders. *Oecologia, 170*(4), 979–986. [https://doi.org/10.1007/s00442-012-2378-9](https://doi.org/10.1080/00063659909477239)

Nicol-Harper, A., Wood, K., Diamond, T., Major, H., Petersen, A., Tertitski, G., Doncaster, C. P., Ezard, T., & Hilton, G. (2021). Vital rate estimates for the common eider *Somateria mollissima*, a data-rich exemplar of the seaduck tribe. *Ecological Solutions and Evidence, 2*(4), e12108. <https://doi.org/10.1002/2688-8319.12108>

Wood, K. A., Thorstensen, S., Lúðvíksson, S. J., Brides, K., & Petersen, A. (2021).

Long‐term trends in the survival rates of adult female Common Eider *Somateria mollissima* at three colonies in Iceland. *Ibis, 163*(2), 671-683. <https://doi.org/10.1111/ibi.12893>

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# **Appendix C: Recruitment propensities**

Recruitment probabilities were based on (*i*) estimates of breeding propensity at 2 years old, 3 years old (including repeat breeders) etc.; and (*ii*) estimates of proportion of recruits first breeding at each age (which must sum to 1 across all ages). The two types of estimate can be combined through the following equality: the proportion of individuals that first breed at age *x* is equal to the proportion that survive to age *x* (without yet breeding) and then breed at age *x*. Since we have survival rates, and do not need to know the proportion of individuals that recruit, we can solve simultaneous equations for the breeding propensity at age *x* for 2 ≤ *x* ≥ 4 (with breeding propensity at 5 years old set to 1, since there is no evidence of any recruitment beyond age 5). The resulting set of simultaneous equations simplifies algebraically to give the age-specific breeding propensities in terms of survival rates and probabilities of first breeding at age *x*. The validity of these calculations was checked via back-substitution, ascertaining that the proportion of 1-year-olds going on to recruit tallies with the complement of the proportion of individuals dying before breeding (at any of 2, 3, 4 or 5 years old). Calculations available upon request.

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# **Appendix D: Comparative analysis across additional published studies**

Here we consider the generality of our results from the common eider case study through comparative re-analyses, applying our elasticity-study effort workflow to the published demographic meta-analyses detailed below (methods adapted from section 2.2 as detailed for each example). Note that we selected demographic meta-analyses with associated MPMs to facilitate direct comparison. Outputs can be replicated with our provided R code.

1. **Vonesh & de la Cruz (2002) – amphibians:**

This study considers “two amphibians with contrasting life-history strategies” (Western toad, *Bufo boreas*, and long-toed salamander, *Ambystoma macrodactylum*), through application of a ‘generalized amphibian life cycle’ (p. 325). We used ‘Fixed’ estimates from their Table 2 to parameterise the provided matrix (their Eqn. 3) for each species (see Table D.1). Study-effort fractions were based on the references in their Table 2; while their study is not strictly a meta-analysis, most transitions are based on information from multiple studies (see Table D.2). Juvenile non/maturation transitions were pooled for the comparison as they are based on the same vital rates and therefore shared study effort.

Table D.1. MPMs for (a) Western toad and (b) long-toed salamander, as derived from Equation 3 and Table 2 in Vonesh & de la Cruz (2002) and Table D.2 below. These are generated in our provided R script as ‘matrix1’, with a prompt for the user to select the species (‘n = 1’ for Western toad or ‘n = 2’ for long-toed salamander). For both species, the matrix transition rates are defined as follows:

[1,1]: juvenile non-maturation = juvenile survival × (1 – maturation)

[1,2]: reproduction = clutch size × egg survival × metamorph survival × density-dependent coefficient × maximum larval survival × sex ratio (assumed equal)

[2,1]: juvenile maturation = juvenile survival × maturation

[2,2]: stasis = adult survival

|  |  |  |
| --- | --- | --- |
| a) | juvenile | adult |
| juvenile | 0.150 | 4.032 |
| adult | 0.050 | 0.600 |

[1,1]: 0.2 × (1 – 0.25); [1,2]: 12000 × 0.6 × 0.2 × 0.007 × 0.8 × 0.5; [2,1]: 0.2 × 0.25

|  |  |  |
| --- | --- | --- |
| b) | juvenile | adult |
| juvenile | 0.348 | 0.648 |
| adult | 0.252 | 0.600 |

[1,1]: 0.6 × (1 – 0.42); [1,2]: 90 × 0.6 × 0.6 × 0.05 × 0.8 × 0.5; [2,1]: 0.6 × 0.42

Table D.2. Summary of information extracted from Vonesh & de la Cruz (2002). WT = Western toad; LTS = long-toed salamander.

|  |  |  |  |
| --- | --- | --- | --- |
| **Matrix element/**  **Transition** | **Contributing vital rates** | **Number of studies** | **References** |
| [1,1]  juvenile 🡪 juvenile (non-maturation) | Juvenile survival; Maturation probability | WT: 3 LTS: 1 | WT: Bayliss, 1994; Clarke, 1977; Nussbaum *et al*., 1983 LTS: Russell *et al*., 1996 |
| [1,2]  adult 🡪 juvenile (reproduction) | Clutch size; Egg survival; Metamorph survival; Density-dependent coefficient; Maximum larval survival; Sex ratio (assumed equal) | WT: 6 LTS: 5 | WT: Nussbaum *et al*., 1983; Blaustein *et al*., 1994; Bayliss 1994; Clarke, 1977; Brockelman, 1969; Wilbur, 1977 LTS: Nussbaum *et al*., 1983; Blaustein *et al*., 1997; Russell *et al*., 1996; Van Buskirk & Smith, 1991; Petranka, 1989 |
| [2,1]  juvenile 🡪 adult (maturation) | Juvenile survival; Maturation probability | WT: 3 LTS: 1 | WT: 3 (Bayliss, 1994; Clarke, 1977; Nussbaum *et al*., 1983) LTS: 1 (Russell *et al*., 1996) |
| [2,2]  adult 🡪 adult (stasis) | Adult survival | WT: 2 LTS: 1 | WT: Olson, 1988; Schmidt & Anholt, 1999 LTS: Russell *et al*., 1996 |

For both species, adult survival was relatively understudied while adult fertility was relatively overstudied (Fig. D.1); the study results confirm greater sensitivity to post-embryonic survival than egg survival (a component of fertility) across a range of density-dependence scenarios. For long-toed salamander, all five studies contributed to adult fertility, so the study-effort fraction is 1.

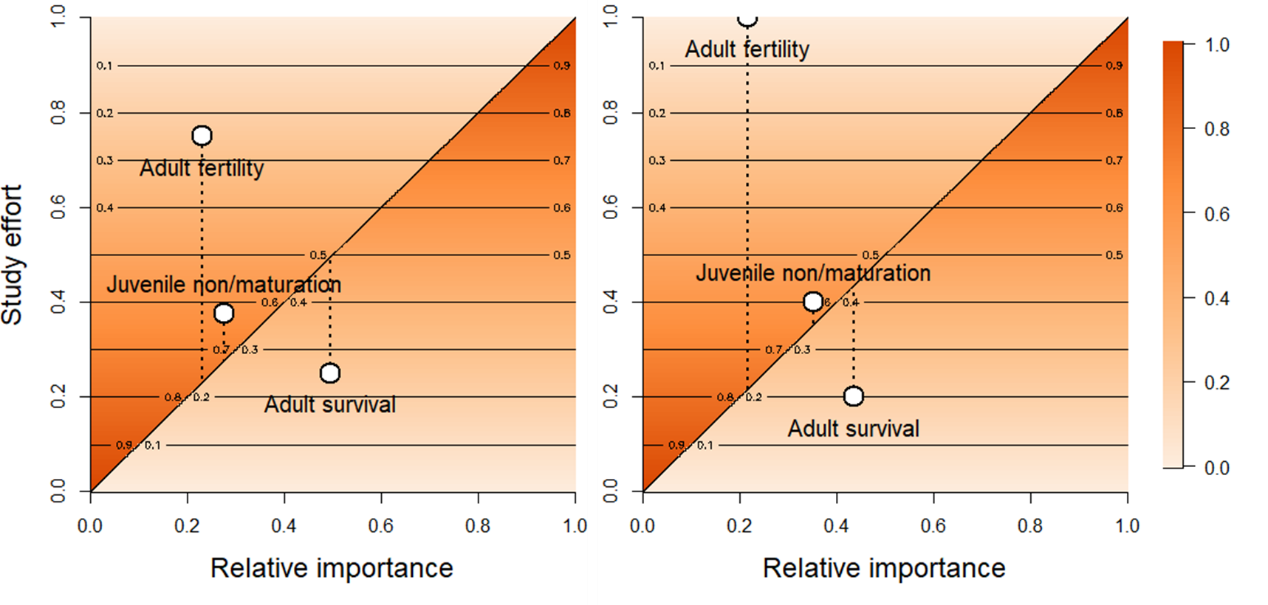


Figure D.1. Cross-plot illustrating study-effort fractions against relative importance as measured by matrix-element elasticities (as for Fig. 4 in the main text), across amphibian life-cycle transitions, for Western toad (left) and long-toed salamander (right). For study-effort fraction numerators, see ‘Number of studies’ in Table D.1; for denominators i.e. total studies: Western toad *n* = 8, long-toed salamander *n* = 5.

1. **Boyce *et al*. (2005) – spotted owl:**

This study refers to three data summaries (Anderson & Burnham, 1992; Burnham, Anderson & White, 1996; Franklin *et al*., 1999) all covering juvenile survival, adult survival and adult fecundity, with overlapping study areas such that the results are non-independent (see their Tables 2 and 3; e.g. presumably the values for study area CAL in the year 1999 meta-analysis include some of the contributing studies for the 1996 and/or 1992 analyses). Given that 22 or 23 of the total 23 sites contribute to each vital rate in at least one summary, this essentially represents a case where all three vital rates have been measured in each study, i.e. study-effort fractions equal to 1 (or 22/23). Hence there is no need to plot a comparative figure, since all vital rates would appear ‘overstudied’, as opposed to having almost equal (near complete) coverage.

1. **Beston (2011) – black bear:**

This study describes a demographic meta-analysis for black bear across North America. We used the values provided on p. 1591 for study-effort fractions (see Fig. D.2 legend) and their Table 5 for vital-rate elasticities (taking a simple mean across the two geographic areas); see Table D.3. Plotting these directly, all transitions are shown to be ‘overstudied’, but especially cub survival and fecundity (Fig. D.2). In this case the recommendation might be for studies that are not able to calculate all parameters to prioritise sub/adult survival at the expense of fecundity and cub survival.

Table D.3 Summary of information extracted from Beston (2011).

|  |  |  |
| --- | --- | --- |
| **Vital rate** | **Number of studies; total = 76** | **Provided elasticities (mean)** |
| Cub survival | 55 | 0.07-0.11 (0.09) |
| Yearling survival | 23 | 0.07-0.11 (0.09) |
| Subadult survival | 23 | 0.20-0.22 (0.21) |
| Adult survival | 52 | 0.55-0.67 (0.61) |
| Fecundity | 32 | 0.07-0.11 (0.09) |

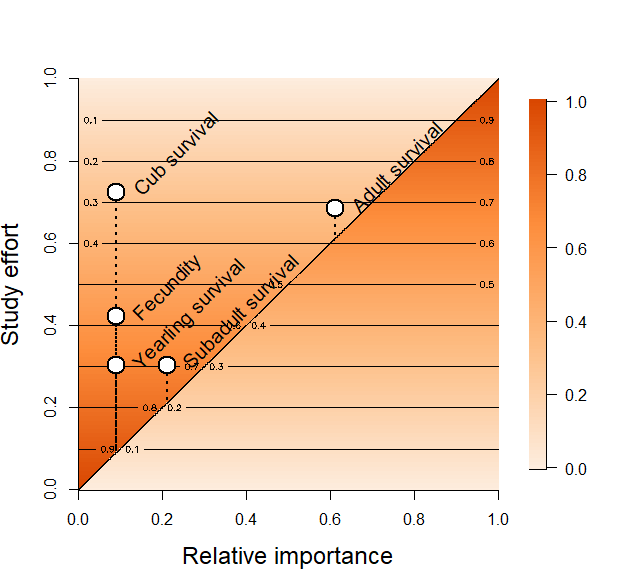


Figure D.2. Cross-plot illustrating study-effort fractions against relative importance as measured by matrix-element elasticities (as for Fig. 4 in the main text), across black bear life-cycle transitions. See Table D.3 for study-effort values.

**Literature cited:**

Anderson, D. R., & Burnham, K. P. (1992). Demographic analysis of northern spotted owl populations. Draft Recovery Plan for the Northern Spotted Owl, Appendix C, pp. 319– 328. US Department of Interior, Fish and Wildlife Service, Portland, OR. (as cited in Boyce *et al*., 2005)

Beston, J. A. (2011). Variation in life history and demography of the American black bear. *Journal of Wildlife Management, 75*(7), 1588–1596. <http://doi.org/10.1002/jwmg.195>

Boyce, M. S., Irwin, L. L., & Barker, R. (2005). Demographic meta-analysis: synthesizing vital rates for spotted owls. *Journal of Applied Ecology, 42*(1), 38–49. <https://doi.org/10.1111/j.1365-2664.2004.00986.x>

Burnham, K. P., Anderson, D. R., & White, G. C. (1996). Meta-analysis of vital rates of the northern spotted owl. *Studies in Avian Biology, 17*, 92–101. (as cited in Boyce *et al*., 2005)

Franklin, A. B. (1992). Population regulation in northern spotted owls: theoretical implications for management. *Wildlife 2000: Populations* (eds D.R. McCullough & R.H. Barrett), pp. 815–830. Elsevier Applied Science, London, UK. (as cited in Boyce *et al*., 2005)

Vonesh, J. R., & De la Cruz, O. (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia, 133*(3), 325–333. <https://doi.org/10.1007/S00442-002-1039-9>

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# **Appendix E: Meta-analysis forest plots and funnel plots**

|  |
| --- |
| **Adult survival:** |
|  |
| Figure E.1. Forest plot for the meta-analysis of adult survival. Squares show the estimate associated with each study, with size proportional to weighting; whiskers show the 95% confidence intervals around these estimates, based on associated sample sizes and overall mean variance. The diamond and vertical line show the weighted mean resulting from the meta-analysis. An asterisk denotes mean estimates based on sub-meta-analyses*.*    Figure E.2. Funnel plot for the meta-analysis of adult survival, with each estimate (observed outcome) represented by a dot. The solid line shows the overall weighted mean, and the dashed line indicates 1. The white area bounded by a dotted line represents the 90% confidence interval; light grey 95%; and dark grey 99%. |
| **Clutch size:** |
| Figure E.3. Forest plot for the meta-analysis of clutch size. Details as for Figure E.1. |
| Figure E.4. Funnel plot for the meta-analysis of clutch size. Details as for Figure E.2, without the vertical line for 1 as clutch size is not a probability. |

|  |
| --- |
| **Hatching success:** |
| Figure E.5. Forest plot for the meta-analysis of hatching success. Details as for Figure E.1. |
| Figure E.6. Funnel plot for the meta-analysis of hatching success. Details as for Figure E.2. |

**Literature cited:**

See ‘Data sources’ in Nicol-Harper *et al*. (2021):

Nicol-Harper, A., Wood, K., Diamond, T., Major, H., Petersen, A., Tertitski, G., Doncaster, C. P., Ezard, T., & Hilton, G. (2021). Vital rate estimates for the common eider *Somateria mollissima*, a data-rich exemplar of the seaduck tribe. *Ecological Solutions and Evidence, 2*(4), e12108. <https://doi.org/10.1002/2688-8319.12108>