Conservation demography: demographic and life-history based frameworks for assessing extinction risk

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To Duncan and Alison

Summary

The biodiversity crisis demands urgent identification of at-risk species, to ensure timely and focused conservation intervention. Demographic modelling contributes to understanding population responses to threats such as over-exploitation and environmental change, but is hindered by incomplete and biased data and limited understanding of how life cycle processes and life history shape demographic responses. Here, I explore barriers to and opportunities for effective conservation demography, using core life history and modelling principles to address limitations and opportunities presented by existing demographic data sets and by relating demographic responses to life history. I focus on long-lived birds, which include many highly threatened species and may present challenges for modelling because of missing stage-specific data due to aspects of their life cycle and habitat use. In Chapter 2, I develop a two-sex model for monogamous species to explore whether including pairing and divorce processes influences insights from classical conservation analyses. When divorce costs take the form of loss of reproductive output, population dynamics in slow-lived species were largely insensitive to pairing and divorce. In Chapter 3, I use phylogenetic imputation to reconstruct vital rates of survival, growth, and reproduction in avian demographic data for use in conservation analyses. Certain vital rates, such as adult survival, could be imputed relatively accurately based on vital rate covariation, with phylogeny and auxiliary trait data improving estimates in some cases. However, demographic metrics such as generation time were sensitive to the accuracy of imputed vital rates. In Chapter 4, I explore the use of pace of life indicators to assess responses to mortality impacts in seabirds. Pace of life indicators could help to assess risk to seabirds from extrinsic threats, reducing dependency on classical vital rates required to parameterise demographic models. Finally, in Chapter 5, I review the literature on demographic responses to climate in mammals to highlight data gaps and limitations for exploring species’ responses to environmental change, revealing geographic and taxonomic biases in missing data and complex demographic responses to climate.

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Statement of intellectual contribution

The work in this thesis would not have been possible without the intellectual contributions of several collaborators. All data chapters are presented as manuscripts for publication. The major contribution of the candidate and the other authors to this work has been explicitly indicated below. Additional contributions are noted in the acknowledgement sections at the end of each data chapter.

Chapter 2 T.D.J., D.Z.C. and A.P.B. conceived and designed the study. T.D.J. implemented the model, carried out the analysis and led the writing of the manuscript. D.Z.C. and A.P.B. contributed critically to the drafts and gave final approval for publication.

Chapter 3 T.D.J., R.S.G., O.R.J., D.Z.C. and A.P.B. designed the study. T.D.J. prepared the data, carried out the analysis and wrote the manuscript. All co-authors provided critical feedback and approved the manuscript for publication.

Chapter 4 T.D.J., D.Z.C. and A.P.B. conceived and designed the study. T.D.J. performed data collection, carried out the analysis and wrote the manuscript. D.Z.C. and A.P.B. contributed critically to the drafts and gave final approval for publication.

Chapter 5 M.P., T.D.J., G.R., and R.S.-G. devised the overall manuscript. M.P. and T.D.J. designed the literature review protocol, which was then implemented by M.P., T.D.J., G.R., C.R.A., S.L., A.M., J.C., N.S.G., J.M.B., and A.P. The climatic data were derived by A.C. The first draft of the manuscript was written by M.P. and R.S.-G., and all co-authors contributed to the final manuscript.

Declaration

This thesis contains original work and does not contain material previously published or written by other persons, except where due reference has been made in the text. The contribution of collaborators to the conceptualisation, data collection, statistical analysis, authorship, and editing of this thesis has been clearly stated. The thesis content results from work I have undertaken since starting my research higher degree and includes no work submitted to qualify for any other degree or diploma in any university or other institution. I have clearly stated which parts of the thesis have been submitted for scientific publication and have obtained the required permissions to include this work. I acknowledge that copyright of the thesis content resides with the copyright holder(s) of that material.

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Chapter 1

General introduction

1.1 Biodiversity crisis and the need for informed conservation action

Globally, biodiversity is in crisis: human activities such as land-use change and exploitation have driven increasing rates of extinction (Barnosky et al. 2011, Pimm et al. 2014, Ceballos et al. 2015), with risks projected to increase in the future with continuing human population expansion (Tilman et al. 2017) and climate change (Parmesan 2006, Maclean and Wilson 2011, Urban 2015). Human-induced threats to biodiversity range from over-exploitation and agriculture to activities associated with economic development such as transport, energy production and urban development (Maxwell et al. 2016, Tilman et al. 2017, Newbold et al. 2018). Species facing multiple threats may be at elevated risk (Brook et al. 2008); for example, climate change has the potential to exacerbate the impact of other threats (Tremblay et al. 2018). Biodiversity loss has consequences for resource availability, ecosystem functioning and resilience, health, and livelihoods (Isbell et al. 2017, Newbold et al. 2018).

The biodiversity crisis demands urgent attention to be brought to the question of which species are at risk (Collen et al. 2011), to ensure timely and focused conservation intervention (Wilson et al. 2007). In the case of vulnerable populations, rapid action may be required to avoid extinction (Martin et al. 2012), so robust decision-making processes are vital (Regan et al. 2005, Bottrill et al. 2008). Successful management of vulnerable populations requires an understanding of how populations will respond, both in the long and short term, to management actions (Law et al. 2017). Furthermore, conservation management is subject to economic and societal constraints which may influence the outcomes of proposed interventions (Armsworth et al. 2011, Lee and Iwasa 2013).

Conservation modelling tools provide a framework for robust decision-making, and techniques such as adaptive management (McCarthy and Possingham 2007, Rout et al. 2009, McDonald-Madden et al. 2010) and expert elicitation (Martin et al. 2005) can be used to guide decision-making even when information is limited. Demographic modelling has become central to addressing questions about managing populations to minimise extinction risk, for example through sensitivity and elasticity analysis (McCarthy et al. 1995, Benton and Grant 1999, de Kroon et al. 2000), population viability analysis (Gilpin and Soule 1986, Lindenmayer et al. 1993, Burgman and Possingham 2000) and optimisation models (Haight 1995, Haight et al. 2002, Yokomizo et al. 2003). Moreover, demographic model outputs, which include population metrics such as population growth rate and estimates of life history parameters such as generation time and age at maturity, are used in frameworks for assessing conservation threat status, notably the IUCN Red List (Mace et al. 2008, IUCN 2020). Here, we provide an overview of demographic modelling tools, discuss their use in conservation decision-making and consider barriers to and opportunities for effective conservation demography.

1.2 Tools for conservation demography

1.2.1 Demographic models

The use of demographic models to guide conservation management is well-established (Wisdom and Mills 1997, Beissinger and Westphal 1998). Demographic models provide a link between individuals and populations. Individual state is the representation of individuals within a population by a set of variables (e.g. age, size, life cycle stage), collectively known as the *i*-state, that characterise variation in individual-level responses to the environment. Population state, or *p*-state, describes the distribution of individuals among different *i*-states. Linking *i*-state to *p*-state is possible under two conditions: firstly, that all individuals are subject to the same environment, and secondly, that the population influences the environment in a way that can be described by additive contributions from the individuals in the population (Metz and Diekmann 1986, Caswell 2001). Structured demographic models, such as matrix population models (Caswell 2001), model the distribution of individual state (e.g. size or age) within a population and provide a framework for scaling up individual-level processes to the population level. Empirical, individual-based data linking individual state to individual performance in a given environment is used to parameterise such models, which can then be used to explore how individual state variation influences population level dynamics. For example, demographic models can be used to predict population performance and to assess the relative merits of alternative management options (e.g. Crouse et al. 1987, Doak et al. 1994).

Analyses based on matrix population models parameterised with estimates of vital rates of survival, growth, and reproduction are widely used to answer questions about how a population will respond to perturbations to vital rates (Selwood et al. 2015). Analytical outputs describe properties of the system such as long-term population growth rate, population structure and reproductive potential, while further characteristics, such as variances associated with stochastic variation in vital rates, can be derived through simulations, leading to a wealth of tools for exploring population dynamics (Wisdom et al. 2000, Caswell 2001, 2007, Koons et al. 2007, Stott 2016).

Typical conservation demographic analyses using matrix population models include classical sensitivity and elasticity analyses, which are used to assess the influence of the underlying vital rates on population growth rate (de Kroon et al. 1986, 2000), and the evaluation of extinction risk under different scenarios, represented by adjustments to model parameters (e.g. Doak et al. 1994, Ginsberg and Milner-Gulland 1994, Menges and Quintana-Ascencio 2004). Matrix models also allow exploration of short-term dynamics arising from perturbations to the stable population structure (Stott et al. 2011). Such deterministic modelling explores population dynamics assuming that vital rates have fixed values. However, in natural populations, vital rates fluctuate from year to year due to changing environmental conditions. Stochastic variation in vital rates is captured by incorporating the range of variability in and covariation among vital rates into the modelling framework. Stochastic population dynamics can be captured through stochastic analytical approaches (Fieberg and Ellner 2001, Lande et al. 2003, Tuljapurkar et al. 2003) or using simulation approaches which also allow exploration of the sensitivities and elasticities of the stochastic population growth rate (e.g. Wisdom et al. 2000, Åberg et al. 2009).

Integral projection models (IPMs, Easterling et al. 2000) provide a modelling framework in which vital rates are linked to a continuous trait distribution, rather than being specified explicitly for discrete classes as in matrix population models. This framework enables analyses equivalent to those for matrix population models (Ellner et al. 2016) and has the benefit of being more tractable than the matrix population model when vital rates depend on a number of state variables (e.g. size and age, Ellner and Rees 2006). Furthermore, integral projection models can incorporate temporal variability and among individual variation in vital rates that can influence population dynamics (Kendall and Fox 2002, Rees and Ellner 2009). However, integral projection models have rarely been applied in a conservation setting (Ferrer-Cervantes et al. 2012, Wallace et al. 2013), perhaps due to perceived complexity of implementation.

1.2.2 Demographic metrics

Demographic models enable the calculation of a range of defining characteristics of a population such as population growth rate and its sensitivities and elasticities to underlying parameters. They allow estimation of derived metrics that capture aspects of life history, such as age at maturation, generation time, and longevity. Generation time is a key metric of species' population dynamics (Frankham and Brook 2004, Sæther et al. 2005) which can be applied to assessments of extinction risk (O'Grady et al. 2008) and which plays an important role in conservation assessments such as the IUCN Red List assessment (Mace et al. 2008). The metric is used as a scaling factor for the period over which to assess population trends, allowing this timescale to be adjusted to account for differences in life history (Mace et al. 2008, IUCN Standards and Petitions Subcommittee 2019). Accurate estimation of generation time is vital to ensure that threat statuses are comparable across species and that assessment results in the assignment of an appropriate level of threat.

1.3 How demographic analysis can help to guide conservation interventions

1.3.1 Sensitivity and elasticity analysis

A canonical example of the application of demographic analysis in a conservation setting is classical sensitivity analysis (Wisdom and Mills 1997). Sensitivity analysis is used to assess the influence of the underlying vital rates of survival, growth, and reproduction on population performance metrics such as population growth rate (de Kroon et al. 1986, 2000). The sensitivity of population growth rate λ to a vital rate s measures the change in λ induced by a small change in s. Sensitivity captures the responsiveness of λ to absolute changes in a vital rate, thereby indicating which vital rates could be targeted by management efforts. However, sensitivity results may be misleading because vital rates measured on different scales are not directly comparable when the same absolute change in the vital rates is not proportionally equivalent (de Kroon et al. 1986). Compare, for example, survival probability, which is measured on a scale between 0 and 1, with fecundity, which must be positive but could be far greater than 1. For this reason, the sensitivity of λ to a proportional change in the vital rate, known as the elasticity, may be preferred, as this measure allows meaningful comparisons among vital rates. Alternatively, survival probabilities can be logarithmically transformed to obtain the time-averaged mortality hazard rate, which measures mortality risk on a ratio scale and allows easier interpretation of elasticities (Ergon et al. 2018). Unlike survival probabilities, a proportional change in mortality hazard rate is independent of the baseline value of the rate, and in discrete time models, elasticity of λ to mortality hazard rate is independent of step length. Analytical formulae exist to calculate sensitivities and elasticities of population growth rate to stage-based transitions and underlying vital rates for deterministic matrix population models (Caswell 2001).

1.3.2 Transient analysis

Transient dynamics describe the short-term responses of a population which has been perturbed from its stable size or structure (Fox and Gurevitch 2000). Transient responses capture adjustments as a population returns to its stable state following disturbance. Short-term dynamics can differ markedly from asymptotic population dynamics and an appreciation of the potential for transient fluctuations is vital to conservation management, which is often focused on short-term interventions and where unexpected transient responses would be unwelcome (Fox and Gurevitch 2000, Koons et al. 2005, Stott et al. 2012). Transient responses include both asymptotic and transient components (Haridas and Tuljapurkar 2007, Stott 2016). Differentiating these effects provides a comprehensive understanding of the short-term impacts of perturbations to population structure. Following a perturbation, the transient dynamics of a population which does not have a stable structure can be very different from those of a population close to a stable stage distribution, so if the initial population structure is not taken into account, predictions of transient responses may be inaccurate and lead to inappropriate management actions.

1.3.3 Population viability analysis

Population viability analysis (PVA) uses stochastic simulations to estimate the probability that a population will persist within a given time frame (Morris and Doak 2002). To perform a demographic PVA (that is, a PVA for a structured population), a structured population model is parameterised using vital rates sampled from suitable distributions, ideally based on empirical estimates of means and associated variance for the target population. PVA can be used to quantify extinction risk under different assumptions about how vital rates may be affected by pressures such as habitat loss, poaching, and environmental change, and allows different management actions to be compared (Doak et al. 1994, Crowder et al. 1994, Menges and Quintana-Ascencio 2004). PVA, whether based on count data or on demographic models, provides numeric outputs that may be used in broader modelling frameworks to allow assessment of the cost-effectiveness of investments into alternative management options (e.g. Duca et al. 2009, Di Minin et al. 2015). While there are caveats to the use of demographic PVA for endangered species due to concerns about data quality and parameter uncertainty (Beissinger and Westphal 1998, Morris and Doak 2002), the technique is accepted as a useful demographic modelling tool (Burgman and Possingham 2000) and is frequently used in conservation planning processes (e.g. Morris et al. 2002).

1.3.4 Optimisation models for conservation prioritisation

Optimisation problems involve maximising or minimising a formal measure of performance, based on the management aims for the system under consideration, subject to a set of constraints (Billionnet 2013). Optimisation is typically applied to find cost-effective management strategies that promote species or population persistence through the selection of defined management interventions (e.g. Duca et al. 2009). In such applications, measuring the impact of interventions on demographic performance is necessary to allow assessment of alternative strategies, hence demographic modelling is a key component of this approach.

Framing conservation management as an optimisation problem allows assessment of management options to account for budgetary constraints. This approach can be used to make a case for selecting particular conservation actions, including the value of additional learning (Rout et al. 2009) and the advantage of economic incentivisation (Di Minin et al. 2015). Bio-economic modelling (Mouysset et al. 2011, 2014) may be a powerful tool for presenting the case for conservation measures to decision-makers.

1.4 Barriers to and opportunities for effective conservation demography

Conservation modelling can be used to determine likely outcomes of proposed interventions, providing guidance without requiring costly (in terms of both time and resources) experimentation on the ground, which may not be possible for endangered and threatened species. However, concerns about applying demographic modelling techniques in a conservation setting have long been recognised (Beissinger and Westphal 1998, Mills et al. 1999, Burgman and Possingham 2000, Coulson et al. 2001). The empirical data required to build demographic models can be difficult to gather, particularly for endangered species (Coulson et al. 2001), and poor data quality can compromise the robustness of quantitative risk assessments carried out using such models (Beissinger and Westphal 1998, Mills et al. 1999, Fieberg and Ellner 2000, Ellner et al. 2002). Structural and parametric uncertainty is inherent in demographic models, and this uncertainty must be handled appropriately to provide an accurate assessment of uncertainty in the model outputs (Burgman and Possingham 2000). Although some have questioned the validity of population viability analysis (Coulson et al. 2001), best practices for implementing this approach have been developed which allow application of this tool (Burgman and Possingham 2000, Reed et al. 2002, McCarthy et al. 2003). Despite this, repeatability and reproducibility of PVAs is low (Morrison et al. 2016), casting doubt on their reliability for conservation decision-making.

Sensitivity and elasticity analyses are powerful tools for identifying appropriate targets for conservation efforts but also require detailed demographic data for the population of interest. Furthermore, caution is required when applying the results of such analyses, which estimate responses as linear changes and are only valid in the vicinity of the demographic model's parameter values. Nonlinear responses are likely in reality due to frequency dependence, density dependence, and transient effects and these could lead to key differences between predicted and actual outcomes (Grant and Benton 2000, Haridas and Tuljapurkar 2007, Stott et al. 2012, Haridas et al. 2014). A further consideration is whether the changes to vital rates that would induce the desired response in population growth rate are feasible.

Constraints on life history traits may result in low variability in certain vital rates (Benton and Grant 1999, Péron et al. 2016). If the vital rates indicated by sensitivity or elasticity analysis as potential targets of management are constrained then management actions targeting those vital rates may have limited success.

In many cases, the detailed demographic data required to calculate important metrics such as generation time are not available. In the absence of such data, proxies based on simpler and more readily available life history data may be used to approximate generation time (IUCN Standards and Petitions Subcommittee 2019). When even these life history estimates are not available, the use of imputation to reconstruct underlying parameters for the calculation of generation time proxies can be a pragmatic approach to obtain maximum coverage of species (Pacifici et al. 2013, Cooke et al. 2018). However, biases in proxies for generation time can lead to over- or under-estimation of threat level (Fung and Waples 2017, Staerk et al. 2019).

Under the threat of global climate change, the problem of managing vulnerable populations must take into account not only current threats but also the way in which changes in climate may affect the populations' responses to those threats. Under IPCC projections (IPCC 2014), increases in average temperatures and precipitation and associated changes in the frequency of extreme weather events are predicted. Local and regional changes in climate have been linked to ecological responses affecting ecosystems and associated biodiversity (Parmesan 2006) and are expected to contribute to accelerating extinction risk (Maclean and Wilson 2011, Urban 2015). Understanding the implications of climate change for extinction risk and the potential for species to become invasive is vital for determining how best to preserve biodiversity (Dawson et al. 2011). Demographic modelling allows prediction of species' responses to projected climate change (Jenouvrier et al. 2009, Barbraud et al. 2011). However, linking demographic responses to environmental drivers requires extensive time-series data and sophisticated modelling approaches (Frederiksen et al. 2014, Teller et al. 2016, Hindle et al. 2019).

Given limited demographic knowledge, the development of techniques that combine demographic analysis with other relevant sources of information to inform conservation assessments would be valuable. For example, if we could identify variables that are correlated with the outputs of demographic analyses and for which information is more readily available than the demographic data required to produce such analyses, those variables could act as proxies for the demographic responses in which we are interested. By relating demographic metrics such as the sensitivities and elasticities of population growth rate to underlying vital rates to such proxies we could develop indicators of the risk to populations from perturbations that affect vital rates. Life history traits such as age at maturity have been identified as indicators for population growth in fish and mammals (Hutchings et al. 2012). Life history traits are promising candidates to inform our understanding of demographic responses. Parallels between species can be drawn by assigning them to a "fast-slow" continuum which captures covariation in life history traits such as lifespan, age at maturity, and reproductive effort (Stearns 1983, Read and Harvey 1989). Such life history traits are closely linked to vital rates such as survival, maturation and fecundity (Promislow and Harvey 1990, Sæther and Bakke 2000). The close relationship between vital rates and life history traits, characterised by species' positions on the fast-slow continuum, could inform our approach to demographic modelling and help us to overcome knowledge gaps. Below I outline four applications of demographic and life history knowledge which provide opportunities for effective conservation demography.

1.4.1 Capturing life history constraints

Among-species patterns of life history are a consequence of evolutionary history. For example, in birds, life history is explained by early diversification in the avian lineage (Owens and Bennett 1995). Patterns of covariance among vital rates are thus well-established and may be relatively inflexible due to selective pressures (Blomberg et al. 2003, Revell et al. 2008). Such evolutionary constraints may reflect the ability of species to adapt to pressures. For example, variability in vital rates which have a strong influence on population growth rate tends to be low (Pfister 1998, Péron et al. 2016), so demographic responses to threats may be constrained. Capturing life history constraints on demographic responses can improve understanding of how populations will respond to management, allowing the selection of interventions which maximise the potential for species recovery. Building species' life history into demographic models can be a valuable way to explore the influence of demographic constraints on population dynamics and to explore ecological and evolutionary consequences of aspects of life history (Coulson et al. 2010, Childs et al. 2011).

1.4.2 Overcoming data limitations

Demographic data is sparse for many species (Conde et al. 2019), particularly for species of conservation concern, for which population numbers may be at critically low levels (Burgman et al. 1993). For example, despite being one of the better studied taxonomic groups, detailed age- and stage-specific information for both survival and fertility is available for only 2.4% of bird species, while for 82% of bird species no information about survival is available (Conde et al. 2019). Lack of demographic data for species of conservation concern makes it difficult to parameterise models used to predict population trajectories. Overcoming data deficiency is a major challenge for conservation which requires novel approaches to make the most of available data (Kindsvater et al. 2018). Opportunities include the use of data for well-studied taxa or populations to predict missing values based on hierarchical structures e.g. relatedness or proximity (Thorson et al. 2017, Kindsvater et al. 2018, Horswill et al. 2019). Imputation is a promising approach to overcome the challenge of demographic data deficiency (Conde et al. 2019). Phylogenetic imputation methods, which account for divergence of trait values over evolutionary history, can be used to generate missing values in species-based data. While several studies have demonstrated effective phylogenetic imputation of functional and life history traits (Guénard et al. 2013, Fagan et al. 2013, Penone et al. 2014), such techniques have not been applied directly to demographic data.

1.4.3 Developing life history indicators

Classical sensitivity analysis is often used to assess population responses to changes in species' vital rates. This framework is well-established but its implementation depends on demographic data that may be absent or difficult to collect. If we could identify variables that are correlated with the sensitivities and elasticities of population growth rate to underlying vital rates and for which information is more readily available, those variables could be used as indicators of a population responses to perturbations that affect vital rates. Many such efforts have focused on ecological and behavioural traits (e.g. Furness et al. 2013). However, life history theory predicts trade-offs among vital rates, hence we might expect species with similar life histories to have similar responses to perturbation. Life history can be characterised by combining species trait data such as age at maturity, longevity, and litter or clutch size and such life history metrics may provide suitable proxies for predicting population responses to threats. The development of such life history indicators (Williams et al. 2010, Conti et al. 2014, Sirot et al. 2015) offers the potential to make assessments which are less reliant on detailed empirical studies.

1.4.4 Understanding demographic responses to a changing climate

While climate change is recognised as a driver of extinction risk (Maclean and Wilson 2011, Urban 2015), our understanding of demographic responses to climate change is limited by lack of knowledge about how vital rates of survival, development and reproduction are affected by climatic drivers. Species demonstrate diverse responses to environmental variation and in many cases aspects of an organism's life history can buffer populations against an uncertain environment. However, rapidly changing climatic conditions, increasing frequency of climatic extremes, and interactions with other threats such as habitat loss or over-exploitation could limit species' resilience to climate change. Knowledge of demographic responses to climate drivers is essential to enhancing our understanding of how environmental change will affect global biodiversity.

1.5 Purpose of this thesis

In this thesis I explore barriers to and opportunities for effective conservation demography, exploring limitations and opportunities presented by existing demographic data sets and exploring links between demographic responses and species' life history. I focus on avian species with slow life history, which include highly threatened taxonomic groups such as seabirds and parrots. Avian species of conservation concern typically present challenges for modelling because of missing data on early or late life stages which emerge from aspects of their life cycle and associated habitat use. Species with slow life history are most sensitive to impacts on adult survival and are associated with increased extinction risk (Bennett and Owens 1997). Moreover, aspects of life history including slow maturation rate, strong pair bonding, and small clutch sizes may increase vulnerability of these species to threats which include overexploitation, habitat degradation and climate change.

Demographic modelling can be used to explore how responses to threats or interventions might be influenced by life history. In Chapter 2, I explore demographic constraints on population performance in long-lived species with strong monogamous pair bonds. The objective was to extend the use of two-sex IPMs to inform conservation, focusing on whether information about mating systems and associated pairing dynamics influence insights from classical conservation analyses. The mating system has the potential to influence population dynamics (Schindler et al. 2013) and strong pair bonding may constrain population growth, for example, if a pair bond between individuals of low quality or compatibility leads to reduced productivity or survival. I develop a demographic framework to analyse the effects of pairing and divorce in long-lived monogamous birds and to explore the demographic and population-level consequences of interactions between life history and pairing and divorce dynamics.

To address the need for accurate demographic data to inform conservation, in Chapter 3, I evaluate a novel application of phylogenetic imputation to fill demographic analysis gaps. Accurate estimates of vital rates of survival, growth, and reproduction are required to parameterise population models for use in analyses that seek to predict how populations will respond to threats that perturb vital rates. However, many taxonomic groups suffer from insufficient data on vital rates for specific life stages required to populate such models. For example, age- and stage-specific information for both survival and fertility is available for only 2.4% of bird species (Conde et al. 2019). Data may be missing for specific life stages due to challenges in recording certain parts of the life cycle, such as juvenile survival in species with cryptic or widely dispersing juvenile stages (Weimerskirch 2002, Pike et al. 2008) or adult survival in long-lived species that present obstacles to marking individuals (e.g. parrots). Estimating key demographic metrics and performing even the most basic conservation demographic analyses for at-risk species with such limited data is challenging and can lead to biases (Fung and Waples 2017, Staerk et al. 2019). I explore whether existing standardised avian vital rates can be reconstructed accurately using phylogenetic imputation and whether demographic metrics such as generation time can be estimated accurately when imputed vital rates are included in the calculations.

In Chapter 4, I present a comparative demographic analysis of population dynamics exploring whether pace of life indicators could be used to assess vulnerability to mortality impacts in seabirds. Seabirds provide a valuable case study because they tend to be slow-lived species with low fecundity and long generation times. Life history theory tells us that long-lived species are more sensitive to mortality impacts than short-lived species. Moreover, for these species, demographic data may be limited by geographic and taxonomic biases, logistical barriers, or aspects of the life cycle such as nomadic life stages. Finding methods that make use of more readily available trait data to assess the impact of mortality events on population growth rate would be valuable for conservation assessment purposes. I investigate whether two proxies of pace of life variation can be used as surrogate metrics for assessing long- and short-term population responses to excess mortality, reducing dependency on the classical vital rates required to parameterise matrix models. In combination with ecological and behavioural indicators, pace of life indicators could help in assessing risk to seabirds from extrinsic threats even when direct knowledge of demographic responses is lacking.

Finally, in Chapter 5, as a primary contributor to the sAPROPOS climate and demography working group, I carried out a review of the literature on demographic responses to climate in mammals to highlight data gaps and limitations of the data available for exploring species' responses to climate change. As a primary author, I helped to devise the study, design and implement the literature review protocol, and write the paper and I conducted key analyses exploring how mammalian demographic responses to climate aligned with vulnerability metrics and IUCN threat levels and whether the complexity of responses reflected IUCN assessed climate threat. While climate change is recognised as a pervasive and escalating threat to persistence for many species (Maclean and Wilson 2011, Urban 2015), our understanding of demographic responses to climate change is limited by lack of knowledge about how climate influences vital rates of survival, development and reproduction. We reviewed studies linking demographic rates in mammals, one of the best-studied taxonomic groups, to climatic drivers. Our results uncover geographic and taxonomic biases in missing data and reveal complex demographic responses to climate. We highlight critical gaps in demographic knowledge which hinder a full understanding of mammal population responses to climate change.

1.6 References

Åberg P, Svensson CJ, Caswell H, Pavia H. 2009. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. *Ecological Modelling*, **220**(5), 605–610.

Armsworth PR, Cantú-Salazar L, Parnell M, Davies ZG, Stoneman R. 2011. Management costs for small protected areas and economies of scale in habitat conservation. *Biological Conservation*, **144**(1), 423–429.

Barbraud C, Rivalan P, Inchausti P, Nevoux M, Rolland V, Weimerskirch H. 2011. Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology*, **80**(1), 89–100.

Barnosky AD, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature*, **471**(7336), 51–57.

Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability in endangered species management. *The Journal of Wildlife Management*, **62**(3), 821–841.

Bennett PM, Owens IPF. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **264**(1380), 401–408.

Benton TG, Grant A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution*, **14**(12), 467–471.

Billionnet A. 2013. Mathematical optimization ideas for biodiversity conservation. *European Journal of Operational Research*, **231**(3), 514–534.

Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**(4), 717–745.

Bottrill MC, et al. 2008. Is conservation triage just smart decision making? *Trends in Ecology & Evolution*, **23**(12), 649–654.

Brook BW, Sodhi NS, Bradshaw CJA. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**(8), 453–460.

Burgman M, Possingham H. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. In Young AG, Clarke GM, eds., *Genetics, Demography and Viability of Fragmented Populations*, pp. 97–112. Cambridge University Press, 1st ed.

Burgman MA, Ferson S, Akçakaya HR. 1993. *Risk assessment in conservation biology*. No. 12 in Population and community biology series. Chapman & Hall, London; New York, 1st ed.

Caswell H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Mass., 2nd ed.

Caswell H. 2007. Sensitivity analysis of transient population dynamics. *Ecology Letters*, **10**(1), 1–15.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances*, **1**(5), e1400253.

Childs DZ, Coulson TN, Pemberton JM, Clutton-Brock TH, Rees M. 2011. Predicting trait values and measuring selection in complex life histories: reproductive allocation decisions in Soay sheep. *Ecology Letters*, **14**(10), 985–992.

Collen B, McRae L, Deinet S, De Palma A, Carranza T, Cooper N, Loh J, Baillie JEM. 2011. Predicting how populations decline to extinction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**(1577), 2577–2586.

Conde DA, et al. 2019. Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences*, **116**(19), 9658–9664.

Conti L, Schmidt-Kloiber A, Grenouillet G, Graf W. 2014. A trait-based approach to assess the vulnerability of European aquatic insects to climate change. *Hydrobiologia*, **721**(1), 297–315.

Cooke RSC, Gilbert TC, Riordan P, Mallon D. 2018. Improving generation length estimates for the IUCN Red List. *PLOS ONE*, **13**(1), e0191770.

Coulson T, Mace GM, Hudson E, Possingham H. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution*, **16**(5), 219–221.

Coulson T, Tuljapurkar S, Childs DZ. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology*, **79**(6), 1226–1240.

Crouse DT, Crowder LB, Caswell H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68**(5), 1412–1423.

Crowder LB, Crouse DT, Heppell SS, Martin TH. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, **4**(3), 437–445.

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**(6025), 53–58.

de Kroon H, Plaisier A, van Groenendael J, Caswell H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**(5), 1427–1431.

de Kroon H, van Groenendael J, Ehrlén J. 2000. Elasticities: a review of methods and model limitations. *Ecology*, **81**(3), 607–618.

Di Minin E, Laitila J, Montesino-Pouzols F, Leader-Williams N, Slotow R, Goodman PS, Conway AJ, Moilanen A. 2015. Identification of policies for a sustainable legal trade in rhinoceros horn based on population projection and socioeconomic models. *Conservation Biology*, **29**(2), 545–555.

Doak D, Kareiva P, Klepetka B. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. *Ecological Applications*, **4**(3), 446–460.

Duca C, Yokomizo H, Marini MÂ, Possingham HP. 2009. Cost-efficient conservation for the white-banded tanager (*Neothraupis fasciata*) in the Cerrado, central Brazil. *Biological Conservation*, **142**(3), 563–574.

Easterling MR, Ellner SP, Dixon PM. 2000. Size-specific sensitivity: applying a new structured population model. *Ecology*, **81**(3), 694–708.

Ellner SP, Childs DZ, Rees M. 2016. *Data-driven Modelling of Structured Populations*. Lecture Notes on Mathematical Modelling in the Life Sciences. Springer International Publishing, Cham.

Ellner SP, Fieberg J, Ludwig D, Wilcox C. 2002. Precision of population viability analysis. *Conservation Biology*, **16**(1), 258–261.

Ellner SP, Rees M. 2006. Integral projection models for species with complex demography. *The American Naturalist*, **167**(3), 410–428.

Ergon T, Borgan Ø, Nater CR, Vindenes Y. 2018. The utility of mortality hazard rates in population analyses. *Methods in Ecology and Evolution*, **9**(10), 2046–2056.

Fagan WF, Pearson YE, Larsen EA, Lynch HJ, Turner JB, Staver H, Noble AE, Bewick S, Goldberg EE. 2013. Phylogenetic prediction of the maximum per capita rate of population growth. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**(1763), 20130523.

Ferrer-Cervantes ME, Méndez-González ME, Quintana-Ascencio PF, Dorantes A, Dzib G, Durán R. 2012. Population dynamics of the cactus *Mammillaria gaumeri*: an integral projection model approach. *Population Ecology*, **54**(2), 321–334.

Fieberg J, Ellner SP. 2000. When is it meaningful to estimate an extinction probability? *Ecology*, **81**(7), 2040–2047.

Fieberg J, Ellner SP. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*, **4**(3), 244–266.

Fox GA, Gurevitch J. 2000. Population numbers count: tools for near-term demographic analysis. *The American Naturalist*, **156**(3), 242–256.

Frankham R, Brook BW. 2004. The importance of time scale in conservation biology and ecology. *Annales Zoologici Fennici*, **41**(3), 459–463.

Frederiksen M, Lebreton JD, Pradel R, Choquet R, Gimenez O. 2014. Identifying links between vital rates and environment: a toolbox for the applied ecologist. *Journal of Applied Ecology*, **51**(1), 71–81.

Fung HC, Waples RS. 2017. Performance of IUCN proxies for generation length. *Conservation Biology*, **31**(4), 883–893.

Furness RW, Wade HM, Masden EA. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, **119**, 56–66.

Gilpin M, Soule ME. 1986. Minimum viable populations: processes of species extinction. In Soule ME, ed., *Conservation biology: the science of scarcity and diversity*, pp. 19–34. Sinauer Associates, Sunderland, Mass.

Ginsberg JR, Milner-Gulland EJ. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology*, **8**(1), 157–166.

Grant A, Benton TG. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology*, **81**(3), 680–693.

Guénard G, Legendre P, Peres-Neto P. 2013. Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution*, **4**(12), 1120–1131.

Haight RG. 1995. Comparing extinction risk and economic cost in wildlife conservation planning. *Ecological Applications*, **5**(3), 767–775.

Haight RG, Cypher B, Kelly PA, Phillips S, Possingham HP, Ralls K, Starfield AM, White PJ, Williams D. 2002. Optimizing habitat protection using demographic models of population viability. *Conservation Biology*, **16**(5), 1386–1397.

Haridas CV, Eager EA, Rebarber R, Tenhumberg B. 2014. Frequency-dependent population dynamics: effect of sex ratio and mating system on the elasticity of population growth rate. *Theoretical Population Biology*, **97**, 49–56.

Haridas CV, Tuljapurkar S. 2007. Time, transients and elasticity. *Ecology Letters*, **10**(12), 1143–1153.

Hindle BJ, Pilkington JG, Pemberton JM, Childs DZ. 2019. Cumulative weather effects can impact across the whole life cycle. *Global Change Biology*, **25**(10), 3282–3293.

Horswill C, Kindsvater HK, Juan-Jordá MJ, Dulvy NK, Mangel M, Matthiopoulos J. 2019. Global reconstruction of life-history strategies: a case study using tunas. *Journal of Applied Ecology*, **56**(4), 855–865.

Hutchings JA, Myers RA, García VB, Lucifora LO, Kuparinen A. 2012. Life-history correlates of extinction risk and recovery potential. *Ecological Applications*, **22**(4), 1061–1067.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Tech. rep., IPCC, Geneva, Switzerland.

Isbell F, et al. 2017. Linking the influence and dependence of people on biodiversity across scales. *Nature*, **546**(7656), 65–72.

IUCN. 2020. The IUCN Red List of Threatened Species. Tech. Rep. Version 2020-1, International Union for Conservation of Nature, Gland, Switzerland. Available from https://www.iucnredlist.org (accessed May 2020).

IUCN Standards and Petitions Subcommittee. 2019. Guidelines for using the IUCN Red List categories and criteria. Tech. Rep. Version 14, prepared by the Standards and Petitions Subcommittee. Available from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed November 2019).

Jenouvrier S, Caswell H, Barbraud C, Holland M, Stroeve J, Weimerskirch H. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences*, **106**(6), 1844–1847.

Kendall BE, Fox GA. 2002. Variation among individuals and reduced demographic stochasticity. *Conservation Biology*, **16**(1), 109–116.

Kindsvater HK, Dulvy NK, Horswill C, Juan-Jordá MJ, Mangel M, Matthiopoulos J. 2018. Overcoming the data crisis in biodiversity conservation. *Trends in Ecology & Evolution*, **33**(9), 676–688.

Koons DN, Grand JB, Zinner B, Rockwell RF. 2005. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, **185**(2), 283–297.

Koons DN, Holmes RR, Grand JB. 2007. Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology*, **88**(11), 2857–2867.

Lande R, Engen S, Sæther BE. 2003. *Stochastic population dynamics in ecology and conservation*. Oxford series in ecology and evolution. Oxford University Press, Oxford; New York.

Law EA, et al. 2017. Projecting the performance of conservation interventions. *Biological Conservation*, **215**, 142–151.

Lee JH, Iwasa Y. 2013. Modeling socio-economic aspects of ecosystem management and biodiversity conservation. *Population Ecology*, **56**(1), 27–40.

Lindenmayer DB, Clark TW, Lacy RC, Thomas VC. 1993. Population viability analysis as a tool in wildlife conservation policy: with reference to Australia. *Environmental Management*, **17**(6), 745–758.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland E, Stuart SN. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**(6), 1424–1442.

Maclean IMD, Wilson RJ. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences*, **108**(30), 12337–12342.

Martin TG, Kuhnert PM, Mengersen K, Possingham HP. 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications*, **15**(1), 266–280.

Martin TG, Nally S, Burbidge AA, Arnall S, Garnett ST, Hayward MW, Lumsden LF, Menkhorst P, McDonald-Madden E, Possingham HP. 2012. Acting fast helps avoid extinction. *Conservation Letters*, **5**(4), 274–280.

Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, **536**(7615), 143–145.

McCarthy MA, Andelman SJ, Possingham HP. 2003. Reliability of relative predictions in population viability analysis. *Conservation Biology*, **17**(4), 982–989.

McCarthy MA, Burgman MA, Ferson S. 1995. Sensitivity analysis for models of population viability. *Biological Conservation*, **73**(2), 93–100.

McCarthy MA, Possingham HP. 2007. Active adaptive management for conservation. *Conservation Biology*, **21**(4), 956–963.

McDonald-Madden E, Probert WJM, Hauser CE, Runge MC, Possingham HP, Jones ME, Moore JL, Rout TM, Vesk PA, Wintle BA. 2010. Active adaptive conservation of threatened species in the face of uncertainty. *Ecological Applications*, **20**(5), 1476–1489.

Menges ES, Quintana-Ascencio PF. 2004. Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecological Monographs*, **74**(1), 79–99.

Metz JAJ, Diekmann O. 1986. Formulating models for structured populations. In Levin S, Metz JAJ, Diekmann O, eds., *The Dynamics of Physiologically Structured Populations*, vol. 68 of *Lecture Notes in Biomathematics*, pp. 78–135. Springer, Berlin, Heidelberg.

Mills LS, Doak DF, Wisdom MJ. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, **13**(4), 815–829.

Morris WF, Bloch PL, Hudgens BR, Moyle LC, Stinchcombe JR. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications*, **12**(3), 708–712.

Morris WF, Doak DF. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Mass.

Morrison C, Wardle C, Castley JG. 2016. Repeatability and reproducibility of population viability analysis (PVA) and the implications for threatened species management. *Frontiers in Ecology and Evolution*, **4**.

Mouysset L, Doyen L, Jiguet F. 2014. From population viability analysis to coviability of farmland biodiversity and agriculture. *Conservation Biology*, **28**(1), 187–201.

Mouysset L, Doyen L, Jiguet F, Allaire G, Leger F. 2011. Bio economic modeling for a sustainable management of biodiversity in agricultural lands. *Ecological Economics*, **70**(4), 617–626.

Newbold T, Hudson LN, Contu S, Hill SLL, Beck J, Liu Y, Meyer C, Phillips HRP, Scharlemann JPW, Purvis A. 2018. Widespread winners and narrow-ranged losers: land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, **16**(12), e2006841.

O'Grady JJ, Reed DH, Brook BW, Frankham R. 2008. Extinction risk scales better to generations than to years. *Animal Conservation*, **11**(5), 442–451.

Owens IPF, Bennett PM. 1995. Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **261**(1361), 227–232.

Pacifici M, Santini L, Marco MD, Baisero D, Francucci L, Marasini GG, Visconti P, Rondinini C. 2013. Generation length for mammals. *Nature Conservation*, **5**, 89–94.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**(1), 637–669.

Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC. 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution*, **5**(9), 961–970.

Péron G, et al. 2016. Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution*, **70**(12), 2909–2914.

Pfister CA. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, **95**(1), 213–218.

Pike DA, Pizzatto L, Pike BA, Shine R. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology*, **89**(3), 607–611.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**(6187), 1246752.

Promislow DEL, Harvey PH. 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of Zoology*, **220**(3), 417–437.

Read AF, Harvey PH. 1989. Life history differences among the eutherian radiations. *Journal of Zoology*, **219**(2), 329–353.

Reed JM, Mills LS, Dunning Jr JB, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett MC, Miller P. 2002. Emerging issues in population viability analysis. *Conservation Biology*, **16**(1), 7–19.

Rees M, Ellner SP. 2009. Integral projection models for populations in temporally varying environments. *Ecological Monographs*, **79**(4), 575–594.

Regan HM, Ben-Haim Y, Langford B, Wilson WG, Lundberg P, Andelman SJ, Burgman MA. 2005. Robust decision-making under severe uncertainty for conservation management. *Ecological Applications*, **15**(4), 1471–1477.

Revell LJ, Harmon LJ, Collar DC. 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, **57**(4), 591–601.

Rout TM, Hauser CE, Possingham HP. 2009. Optimal adaptive management for the translocation of a threatened species. *Ecological Applications*, **19**(2), 515–526.

Sæther BE, Bakke Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**(3), 642–653.

Sæther BE, et al. 2005. Generation time and temporal scaling of bird population dynamics. *Nature*, **436**(7047), 99–102.

Schindler S, Neuhaus P, Gaillard JM, Coulson T. 2013. The influence of nonrandom mating on population growth. *The American Naturalist*, **182**(1), 28–41.

Selwood KE, McGeoch MA, Mac Nally R. 2015. The effects of climate change and land-use change on demographic rates and population viability. *Biological Reviews*, **90**(3), 837–853.

Sirot C, Villéger S, Mouillot D, Darnaude AM, Ramos-Miranda J, Flores-Hernandez D, Panfili J. 2015. Combinations of biological attributes predict temporal dynamics of fish species in response to environmental changes. *Ecological Indicators*, **48**, 147–156.

Staerk J, Conde DA, Ronget V, Lemaitre JF, Gaillard JM, Colchero F. 2019. Performance of generation time approximations for extinction risk assessments. *Journal of Applied Ecology*, **56**(6), 1436–1446.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**(2), 173–187.

Stott I. 2016. Perturbation analysis of transient population dynamics using matrix projection models. *Methods in Ecology and Evolution*, **7**(6), 666–678.

Stott I, Hodgson DJ, Townley S. 2012. Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. *Methods in Ecology and Evolution*, **3**(4), 673–684.

Stott I, Townley S, Hodgson DJ. 2011. A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, **14**(9), 959–970.

Teller BJ, Adler PB, Edwards CB, Hooker G, Ellner SP. 2016. Linking demography with drivers: climate and competition. *Methods in Ecology and Evolution*, **7**(2), 171–183.

Thorson JT, Munch SB, Cope JM, Gao J. 2017. Predicting life history parameters for all fishes worldwide. *Ecological Applications*, **27**(8), 2262–2276.

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to biodiversity and pathways to their prevention. *Nature*, **546**(7656), 73–81.

Tremblay JA, Boulanger Y, Cyr D, Taylor AR, Price DT, St-Laurent MH. 2018. Harvesting interacts with climate change to affect future habitat quality of a focal species in eastern Canada’s boreal forest. *PLOS ONE*, **13**(2), e0191645.

Tuljapurkar S, Horvitz CC, Pascarella JB. 2003. The many growth rates and elasticities of populations in random environments. *The American Naturalist*, **162**(4), 489–502.

Urban MC. 2015. Accelerating extinction risk from climate change. *Science*, **348**(6234), 571–573.

Wallace K, Leslie A, Coulson T. 2013. Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology*, **82**(1), 155–165.

Weimerskirch H. 2002. Seabird demography and its relationship with the marine environment. In Schreiber EA, Burger J, eds., *Biology of Marine Birds*, pp. 115–135. CRC Press.

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**(10), 2280–2291.

Wilson KA, et al. 2007. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biol*, **5**(9), e223.

Wisdom MJ, Mills LS. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *The Journal of Wildlife Management*, **61**(2), 302.

Wisdom MJ, Mills LS, Doak DF. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology*, **81**(3), 628–641.

Yokomizo H, Yamashita J, Iwasa Y. 2003. Optimal conservation effort for a population in a stochastic environment. *Journal of Theoretical Biology*, **220**(2), 215–231.

Chapter 2

Individual quality, pairing and divorce processes in monogamous birds

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This manuscript is in preparation for submission to *Oikos*.

Abstract

1. Differences in individual quality are often implicated in pair formation and the dissolution (divorce) of pairs, and interactions between these aspects of mating systems have the potential to influence population stability and persistence.
2. Here, we developed a framework to explore the demographic and population-level consequences of interactions between pairing and divorce processes in long-lived monogamous birds.
3. We applied sensitivity and transient analyses to a sex-symmetric demographic model with an explicit representation of individual quality to explore how pairing and divorce influence short- and long-term population growth rate.
4. We found that the sensitivity of asymptotic population growth rate to most pairing and divorce parameters was low. Transient responses to divorce were similarly restrained, with moderate responses to divorce parameters only for amplification metrics.
5. Pairing and divorce dynamics seem to have minimal influence on population growth rate and transient dynamics in long-lived monogamous species. Other processes, particularly those affecting adult survival, are likely more important in conservation management of such species.

Keywords—divorce, monogamy, assortative pairing, individual quality, heterogeneity, integral projection model.

2.1 Introduction

Successful conservation of populations depends on identifying key sensitivities of population growth rate to the aspects of a species' life cycle that can be realistically managed and using this information to guide conservation actions. In monogamous species, pair formation and the persistence and dynamics of pair bonds are key features of the mating system with the potential to influence population stability and persistence (McNamara et al. 1999, Berec and Boukal 2004). The underlying processes encompass maturation, mortality, pair bonding and divorce (that is, the dissolution of a pair bond in the absence of within-pair mortality) (Parker 1983, Black 1996). These processes are challenging to incorporate into the standard matrix models used in population ecology and conservation biology, because they require specification of both female and male life cycles and inclusion of a set of criteria for pair formation and dissolution (Pollard 1997, Maxin and Berec 2010). Nevertheless, it is pertinent to ask how these processes influence both the long-term stability of populations, as characterised by the asymptotic population growth rate, and short-term responses to perturbations such as those associated with conservation interventions, habitat loss or other human impacts.

Divorce in monogamous birds is widely documented (Ens et al. 1996, Dubois et al. 1998, Dubois and Cézilly 2002), with much variation in rates of divorce among species which form monogamous pair bonds (Rowley 1983, Ens et al. 1996, Dubois and Cézilly 2002, Bried and Jouventin 2002). Mortality rate is a strong predictor of divorce rates in birds (Jeschke and Kokko 2008), indicating that life history plays an important role in determining pair fidelity. Divorce has been shown to have adaptive potential (Culina et al. 2015c), despite the potential costs associated with finding a new partner. The majority of evidence shows that divorce costs manifest in terms of reproduction (Heg et al. 2003, Jeschke et al. 2007, Ismar et al. 2009) rather than survival (but see Culina et al. 2015b, Jankowiak et al. 2018). This suggests that the impact of divorce on population growth rate and transient dynamics is likely to be minimal in long-lived species, for which sensitivity of population growth rate to reproduction is low (Sæther and Bakke 2000). However, divorce rates are typically low in long-lived monogamous species (Dubois et al. 1998, Dubois and Cézilly 2002, Bried and Jouventin 2002), suggesting that there may be additional costs of divorce.

Previous work exploring pairing dynamics can be separated into two groups. Firstly, several studies have concentrated on frequency-dependent aspects of mating systems. Frequency dependence arises in two-sex systems when reproductive rates are dependent on the proportion of females to males. This has led to consideration of the impact of sex differences in demography and frequency dependence in mating opportunities on mating systems (Legendre et al. 1999, Bessa-Gomes et al. 2004, Schindler et al. 2013), sex roles (Kokko and Johnstone 2002, Kokko and Jennions 2008), sex ratios (Veran and Beissinger 2009, Shelton et al. 2010, Shyu and Caswell 2016), sex allocation strategies (Schindler et al. 2015) and trait evolution (Childs et al. 2016). Divorce has been specifically considered in a frequency-dependent setting (Maxin and Berec 2010, Shyu and Caswell 2018), as well as in individual based and game theoretic models exploring ecological and evolutionary constraints on pairing and divorce (McNamara and Forslund 1996, McNamara et al. 1999, Berec and Boukal 2004). These studies address evolutionary and stability questions relating to the relative frequency of females and males in two-sex systems.

Secondly, some studies have investigated extinction risk (Sæther et al. 2004, Berec and Boukal 2004, Lee et al. 2011, Gerber and White 2014, Tsai et al. 2014), and responses to sex-biased harvesting (Traill et al. 2014, Snyder et al. 2014, Shyu and Caswell 2018) and environmental change (Petry 2016, Coulson et al. 2017). These studies tend to consider how constraints of the mating system, again often relating to frequency dependence and demographic sex differences, influence population viability and responses to harvest or environmental perturbations.

Across both groups, the pair formation process is typically specified through a mating function based on pairing between individuals according to stage- or age-based distributions (e.g. Caswell and Weeks 1986, Pollard 1997, Shyu and Caswell 2018). Mating functions are inherently frequency-dependent: the relative frequency of females and males affects the number of pairs formed and, subsequently, reproductive rates. While population growth rate in two-sex systems can be sensitive to frequency-dependent factors such as mate availability (Stephens et al. 2002, Haridas et al. 2014), invoking frequency dependence in two-sex models introduces complexity. In a frequency-dependent setting, the elasticities of population growth rate to underlying vital rates are composed of two parts: the classical elasticity, capturing the effect of a linear change in the vital rate on population growth rate, and a nonlinear component describing the effect of the change on population structure and the resulting changes in vital rates (Caswell 2008, Haridas et al. 2014). However, we wish to focus on the influence of pairing and divorce processes on population growth rate and transient population dynamics in the absence of frequency-dependence.

Consistent individual differences in fitness-related traits such as survival and reproductive success (e.g. Cam et al. 2002, Weladji et al. 2008, Hamel et al. 2009, Fay et al. 2016) are often described by the term *individual quality*. Individual quality is defined formally as a measure of within-individual covariance in vital rates arising due to genetic or environmental factors (Wilson and Nussey 2010, Bergeron et al. 2011). Numerous field studies have provided evidence of differences in individual quality (Lescroël et al. 2009, Moyes et al. 2009, Aubry et al. 2011, Zhang et al. 2015) and the influence of quality on breeding success (Lewis et al. 2006, Fayet et al. 2017) and pair bonding and divorce (Ens et al. 1993, 1996). This suggests that individual quality could be used to capture both pair performance and pair bond formation and maintenance.

Here, we incorporate an explicit representation of individual quality into a demographic framework for pairing and divorce. We assume that male and female vital rates are equal. Under this assumption of symmetric demography, we can investigate the population-level impacts of pairing and divorce in the absence of frequency-dependent processes, avoiding the complexity of nonlinear elasticities. While vital rates vary between sexes in many species, for relatively long-lived species with low levels of sexual dimorphism and equal allocation of parental care, sex differences in vital rates may be relatively small compared to differences arising due to individual heterogeneity (Fay et al. 2016).

In our framework, individual quality acts as a determinant of individual and pair demographic performance, affecting survival and reproduction and governing pairing and divorce dynamics. We assume a system of biparental care with reproductive effort shared equally between the members of a pair, so that the qualities of both members influence reproductive success. Under the assumptions of demographic symmetry and large population size, males and females are equally distributed in terms of individual quality. These conditions allow us to implement a novel, quality assortative pairing method using a multivariate approach from probability theory. Quality assortative pairing arises when pairing decisions are based on mutual mate choice for partner quality (Johnstone 1997). Assortative pairing may improve the compatibility between pair members, potentially improving reproductive success (Lewis et al. 2006) and subsequently influencing patterns of divorce (Culina et al. 2015c).

Furthermore, assortative pairing may result in the formation and continued association of pairs with high reproductive success. Hence, we might expect assortative pairing to have a positive effect on population growth rate.

We consider two alternative aspects of pair quality that may influence divorce rates. Firstly, the effect of within-pair quality may be additive, with greater pair fidelity in pairs with higher mean pair quality. Secondly, within-pair quality differences may produce antagonistic effects, for example through reduced compatibility, which could have a negative influence on pair fidelity. We expect the shape of the pair quality-divorce relationship to influence pair bond duration and hence the stable distribution of pair quality combinations. Since reproductive output is dependent on pair quality, changes in the pair quality distribution brought about by pairing and divorce dynamics may have consequences for population growth rate.

Our model represents the life history of long-lived species which form long-term monogamous partnerships. Pairing and divorce may have a more significant impact on demography in such species, which form strong pair bonds and have relatively long lifespans. We make a comparison between a "slow" life history strategy, with high rates of survival and low fecundity, and a "fast" life history strategy, in which individuals are relatively short-lived but have higher reproductive output. We expect sensitivities to pairing and divorce processes to be related to the impact of divorce costs under these two life history strategies.

We address three fundamental questions. Firstly, is population growth rate sensitive to quality assortative pairing and how does divorce influence this relationship under the two alternative life history strategies? Secondly, how does the relationship between pair quality and divorce influence demographic structure and does this have consequences for population growth rate? Lastly, how do short-term responses to perturbations vary across a range of divorce and pairing parameters and across slow and fast life history strategies?

2.2 Materials and methods

2.2.1 Model characteristics

We consider a monogamous species with a life history representing the "slow" end of the slow-fast continuum (Stearns 1983), consistent with avian groups such as seabirds, raptors

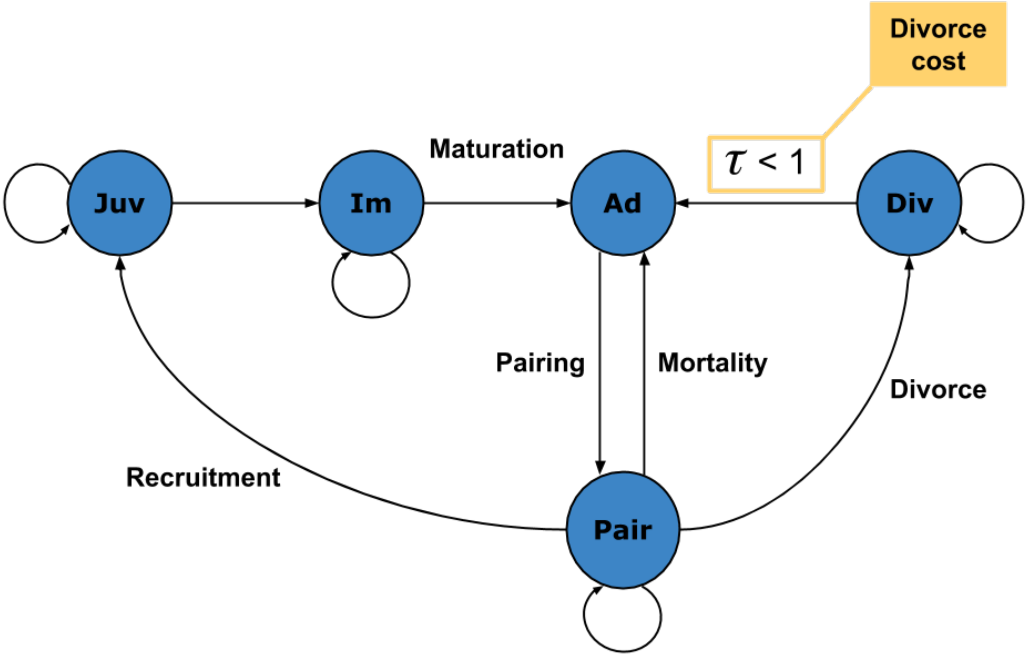

Figure 2.1: Life cycle diagram. Individuals remain unpaired during the juvenile (Juv) and immature (Im) stages. On reaching maturity, individuals join the population of breeding adults (Ad). Pairs are formed from a common pool and may dissolve due to within-pair mortality or divorce. Divorced individuals (Div) are subject to a divorce cost in the form of a delay to re-entering the pairing pool, indicated by the parameter τ.

and parrots. Individuals in these taxa typically form long-term monogamous partnerships and remain paired except under exceptional circumstances: the death or, rarely, divorce of a partner. In this event, individuals form new partnerships, a process which may be costly, for example due to missed breeding opportunities. We assume that, within the successive life stages of juvenile, immature and adult, male and female vital rates are equal. This assumption allows us to examine the intrinsic effects of quality-linked pairing and divorce processes on population growth rate in the absence of frequency-dependent effects.

The life cycle is characterised by high adult survivorship and low annual reproductive output, with breeding commencing after an extended period of immaturity. We identify juvenile, immature and adult stages of development to reflect this life cycle (Fig. 2.1). During the juvenile period, we assume that individuals are subject to higher mortality, while at the immature stage survival rates are similar to those of adults but breeding has not yet commenced. This corresponds to a period of delayed maturation prior to recruitment to the breeding population, as observed in many long-lived species. Once individuals have matured to the adult stage they become available for pairing. We assume that there is a single pairing pool for new recruits and returning adults, so that individuals may form pairs despite differences in age and experience. Further, we assume that there is complete pairing of unpaired adults at each pairing opportunity. Surviving members of pairs which dissolve due to the death of one partner (widowing) re-enter the breeding pool immediately, while divorced individuals may be subject to a delay to re-pairing, which represents the cost of divorce. Pairs which survive and remain together are available to breed again in subsequent breeding seasons.

We use a continuously varying measure of individual quality to describe underlying differences between individuals due to genetic and environmental factors (Hamel et al. 2009, Wilson and Nussey 2010, Fay et al. 2016). We assume that individual quality remains constant over the lifetime of an individual, so that differences between individuals are maintained (Cam et al. 2002, Fay et al. 2017). In addition to determining the demographic traits of individuals, we assume that individual quality is important in pairing and divorce processes, influencing the quality of partners available when pairing, the reproductive output of pairs and the incidence of divorce across the pair quality distribution.

2.2.2 Demographic modelling framework

We extend the integral projection model (IPM) framework (Easterling et al. 2000) to create a demographic model in which the quality of individuals and the joint quality of pairs influence demographic processes. An individual of either sex has a state comprised of its life stage (m, one of J(uvenile), I(mmature), A(dult) or D(ivorced adult)), pair status and individual quality (x). For pairs, partner quality is an additional aspect of state which affects reproductive output and the probability of divorce; we denote the joint quality of a pair by $z = (x_1, x_2)$ where x_1 and x_2 are the individual qualities of the pair members. At the core of the model is a nonlinear, quality-based pairing process which governs the formation of pairs from the available pool of single individuals (Section 2.2.2).

We write $n_m(x,t)$ for the distribution of quality-x single individuals of either sex in life stage m at time t and $n_b(z,t)$ for the distribution of paired individuals in breeding class b with joint quality $z = (x_1, x_2)$ at time t. Integrating $n_m(x,t)$ over a quality interval $\Omega_m = [L, U]$ gives the total number of single individuals in that range. Similarly, the total number

$s_m(x)$	probability of individual survival at stage m
$s_i(z)$	probability of survival of the ith member of a pair of quality z
$s_P(z)$	probability of both members of a pair of quality z surviving
$d(z)$	probability of divorce for pair of quality z
$r(z)$	net recruitment for pair of quality z
$\tau(m',m)$	transition probability
$f(x',z)$	production of offspring of quality x' given parental pair quality z
$C(x',z)$	density of offspring of quality x' given parental pair quality z
$g(x',x)$	density of individuals of quality x' given original quality x
$g(x',z)$	density of individuals of quality x' from dissolution of pair of quality z
$G(z',z)$	bivariate density of pairs of quality z' given original pair quality z

Table 2.1: Demographic component functions and parameters for the IPM kernels.

of paired individuals in a range of pair quality values Ω_b in $\mathbb{R}^2$ at time t is obtained by integrating $n_b(z,t)$ over the specified range. The distribution of individuals at time $t+1$ is given by the system:

$$\begin{aligned} n_{m'}(x',t+1) = {} & \sum_m \int_{\Omega_m} K_{ss}(x',m',x,m)\, n_m(x,t)\, dx \\ & + \sum_b \int_{\Omega_b} \Big[K_f(x',m',z) + K_d(x',m',z)\Big] n_b(z,t)\, dz\,, \end{aligned} \tag{2.1}$$

$$n_{b'}(z',t+1) = \sum_b \int_{\Omega_b} K_s(z',z)\big(n_b(z,t) + \mathcal{P}(n_A(x,t))\big)\, dz\,. \tag{2.2}$$

Here, K_{ss}, K_f, K_d and K_s represent singleton survival, recruitment, pair dissolution and pair survival, respectively, and $\mathcal{P}$ determines the distribution of new pairs formed from the pool of adult individuals. In the following sections, we describe the kernel functions and the quality-linked processes of survival, reproduction, pairing and divorce that underlie these functions. The functions that form the kernel components are summarised in Table 2.1.

Pairing

At the start of each time step, new pairs are formed from the pool of single individuals produced at the previous time step through the recruitment of immature individuals and the dissolution of existing pairs. We generate the pair quality distribution for new pairs using a copula, a multivariate probability distribution that defines a joint distribution of uniform random variables with a specified correlation structure. Copulas are typically used to generate samples from arbitrary distributions which conform to a given correlation structure. Here,

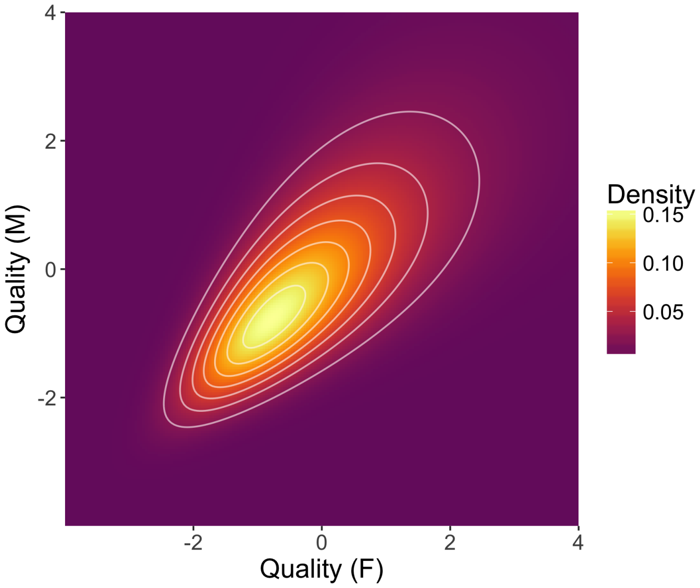

Figure 2.2: Bivariate pair quality distribution formed using a Gaussian copula, arbitrary marginals and pair correlation coefficient $\rho = 0.75$.

we apply a Gaussian copula in reverse to produce a bivariate distribution with a specified correlation, which characterises the strength of assortative pairing, based on the marginal distributions of the individuals available for pairing.

To produce a bivariate distribution for pair quality with a specified level of correlation in quality, ρ, we take the marginal distribution of adult individuals, $n_A(x,t)$, and transform it by calculating its cumulative density and interpolating to produce an empirical cumulative distribution function. This maps the distribution of individual quality to a uniform distribution. We apply a Gaussian copula to link two uniform random variables, u_1 and u_2, through a bivariate normal distribution with the specified correlation parameter $\rho \in [-1,1]$,

$$C_\rho(u) = \Phi_\rho\left(\Phi^{-1}(u_1), \Phi^{-1}(u_2)\right). \tag{2.3}$$

Here, Φ^{-1} is the inverse cumulative distribution function of a standard normal distribution and Φ_ρ is the joint cumulative distribution function of a bivariate normal distribution with correlation parameter ρ. The copula is used to calculate a bivariate probability density across an evenly-spaced grid of uniform values. Finally, rescaling the bivariate density produces a pair quality distribution on the scale of the original variables (Fig. 2.2).

Survival and growth

The first term in equation (2.1) describes the contribution through transitions from all singleton stages to the distribution of singletons of stage m' at the next time step. The singleton survival kernel is given by

$$K_{ss}(x', m', x, m) = s_m(x)\tau(m', m)g(x', x)\,, \tag{2.4}$$

representing individuals that survive, move from stage m to stage m', and grow to quality x' at the next time step. We assume that individual survival at life stage m varies with quality x according to a logistic relationship:

$$s_m(x) = s_{min} + \frac{s_{max} - s_{min}}{1 + e^{\alpha - kx}}, \quad \alpha = \log\left(\frac{s_{max} - \bar{s}_m}{\bar{s}_m - s_{min}}\right). \tag{2.5}$$

Here, s_{min}, s_{max} and $\bar{s}_m$ denote minimum, maximum and mean survival rates for the stage, k is the slope of the relationship, and the location parameter α ensures that the mean survival value occurs at quality $x = 0$. The probability of transition between singleton stages, $\tau(m', m)$, is the reciprocal of the typical stage length, and to ensure that quality remains constant throughout an individual's lifetime, the density function $g(x', x)$ is a Dirac delta function, which takes an infinite value at $x' = x$ and is zero elsewhere.

Equation (2.2) gives the contribution through survival of newly formed and established breeding pairs to the distribution of pairs at the next time step. The pair survival kernel,

$$K_s(z', z) = s_P(z)(1 - d(z))G(z', z)\,, \tag{2.6}$$

denotes pairs that survive, remain together (i.e. do not divorce) and contribute to the pair distribution at the next time step. We assume that members of a pair with joint quality $z = (x_1, x_2)$ survive independently of each other. The probability of both members of a pair surviving equals the product of the survival of the individuals that form the pair:

$$s_P(z) = s_A(x_1)s_A(x_2)\,. \tag{2.7}$$

We model the probability of divorce as a function of pair quality, combining mean pair

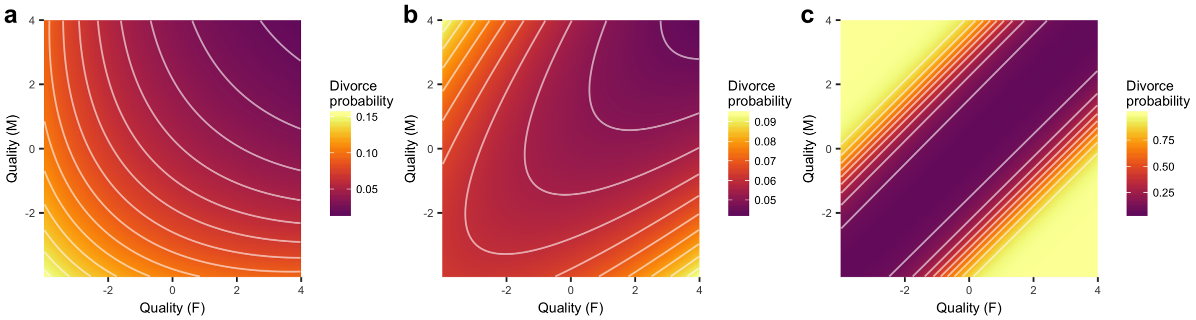

Figure 2.3: The probability of divorce in relation to pair quality under different formulations of the divorce function (Equation 2.8). (a) The mean pair quality term ($\beta = 0.3$) dominates the pair quality difference term ($\gamma = 0.01$); (b) mean pair quality ($\beta = 0.05$) and pair quality difference ($\gamma = 0.01$) have similar influence; (c) the pair quality difference term ($\gamma = 0.3$) overwhelms the mean pair quality term ($\beta = 0.01$).

quality, $\bar{z} = \frac{1}{2}(x_1 + x_2)$, and within-pair quality difference, $\Delta z = |x_1 - x_2|$:

$$d(z) = \text{logit}^{-1}(\alpha - \beta\bar{z} + \gamma\nu\Delta z^2)\,. \tag{2.8}$$

Here, the parameter α defines the baseline divorce rate (as $\text{logit}^{-1}\alpha$), β and γ are, respectively, the influence of mean pair quality and within-pair quality difference on divorce probability, and $\nu = 1/\max(x)$ is a scaling factor that allows β and γ to be varied on the same scale. As mean pair quality increases, divorce rate is reduced, while increasing the difference between members of the pair leads to a greater probability of divorce. The parameter values control the strength of this interaction (Fig. 2.3). As with individual quality, the quality of existing pairs is fixed, so we choose a Dirac delta function for the density $G(z', z)$ so that pair quality remains constant between time steps.

Recruitment, divorce and within-pair mortality

The second term in equation (2.1) contains kernel components for recruitment and pair dissolution. Newly formed pairs, together with existing pairs, participate in the reproduction, mortality and divorce transitions that contribute towards the distribution of singletons at the next time step. The kernel governing recruitment of offspring to the pool of juvenile singletons is given by

$$K_f(x', m', z) = \frac{1}{2}s_P(z)f(x', z)\,, \quad m' = J\,. \tag{2.9}$$

Here, pair survival (2.7) is combined with the production and survival of offspring, summarised by the fecundity subkernel, $f(x',z)$. The factor of half scales the kernel to represent the contribution from each individual member of the pair. The fecundity subkernel in equation (2.9) is given by

$$f(x',z) = \frac{1}{2}r(z)C(x',z)\,. \tag{2.10}$$

This combines the net recruitment of offspring for a pair of a given quality with the offspring quality distribution, assuming an equal sex ratio in recruited offspring. We assume a logistic relationship between mean pair quality and net recruitment to the juvenile stage, with recruitment increasing nonlinearly up to a limit formed by the maximal clutch size. For a pair with quality $z = (x_1, x_2)$, net recruitment is given by

$$r(z) = r_{min} + \frac{r_{max} - r_{min}}{1 + \mathrm{e}^{\alpha - k\bar{z}}}, \quad \alpha = \log\left(\frac{r_{max} - \bar{r}}{\bar{r} - r_{min}}\right), \tag{2.11}$$

where r_{min}, r_{max} and $\bar{r}$ denote the minimum, maximum and mean net recruitment values, $\bar{z} = \frac{1}{2}(x_1 + x_2)$ is mean pair quality, k is the slope of the relationship and the location parameter α ensures that the mean recruitment value occurs at mean pair quality $\bar{z} = 0$. We assume that there is no influence of parental quality on the development of offspring quality; in other words, an individual's quality is determined solely by its environment, with no parental effects. Hence, each individual is assigned a quality at birth, which is retained throughout its lifetime. We select offspring quality $C(x',z)$ from a normal distribution.

The kernel component for pair dissolution in equation (2.1) is composed of two terms:

$$K_d(x',m',z) = \frac{1}{2}\Big(s_i(z) + \frac{1}{2}s_P(z)\,d(z)\,\tau(m',m)\Big)g(x',z)\,,$$
$$m = D,\ m' \in \{A, D\},\ i \in \{1,2\}\,. \tag{2.12}$$

The first term accounts for widowing through the survival of one member of a pair and the second describes the survival (2.7) and divorce (2.8) of a pair to produce a single individual with a given state m'. The outer factor of half scales the kernel to represent the contribution from each individual member of the widowed or divorced pair. The probability of a single member of a pair surviving is a product of the survival and mortality, respectively, of the adults within the pair:

$$s_i(z) = s_A(x_i)(1 - s_A(x_j)), \quad i \in \{1,2\},\ j = 1 + i \bmod 2\,. \tag{2.13}$$

We assume that divorced individuals may suffer a delay to repairing, so that divorce may result in one or more missed breeding opportunities. The return of divorced individuals to the pairing pool is governed by a transition probability $\tau(A, D) = \tau_{D \to A}$ that captures this cost of divorce. Since individual quality is fixed, the density for divorced and widowed individuals, $g(x', z)$, is obtained by marginalising the joint quality distribution for pairs that divorce or suffer within-pair mortality. This formulation maintains individual quality across the pair dissolution event.

2.2.3 Model parameterisation

We parameterised the slow life history model with a set of demographic parameters derived from estimates of life history traits for the yellow-nosed albatross, *Thalassarche chlororhynchos*, as an exemplar of a long-lived monogamous species (Cuthbert et al. 2003, Dubois et al. 1998, Bried and Jouventin 2002). These estimates are typical of values for survival, maturation, reproduction and divorce in Procellariiformes (Schreiber and Burger 2001, Bried and Jouventin 2002). Species in this order are at the "slow" end of the range of life histories seen in seabirds (Schreiber and Burger 2001), while divorce rates are amongst the lowest found in monogamous birds (Ens et al. 1996, Dubois and Cézilly 2002, Bried and Jouventin 2002). We obtained a contrasting "fast" life history by reducing mean survival across all life stages by one third to a half, increasing reproductive output threefold and reducing age at first reproduction by two thirds. We retained the same baseline divorce rate for both life histories since this parameter is varied during the analysis. Table 2.2 lists the full set of model parameters.

2.2.4 Sensitivity analysis

We carried out sensitivity analysis to explore how interactions between pairing and divorce parameters influence population growth rate under the two alternative life history strategies. We varied correlation in pair quality in combination with underlying divorce parameters (baseline divorce rate, influence of mean pair quality, influence of pair quality difference

Parameter	Notation	Value	Reference
Juvenile survival mean	$\bar{s}_J$	0.79 (0.4)	Cuthbert et al. (2003)
Immature survival mean	$\bar{s}_I$	0.88 (0.5)	Cuthbert et al. (2003)
Adult survival mean	$\bar{s}_A$	0.92 (0.65)	Cuthbert et al. (2003)
Minimum survival	s_{min}	0.2	
Maximum survival	s_{max}	0.98	
Survival slope	k_s	0.5	
Net reproductive output mean	$\bar{r}$	0.44 (1.33)	Cuthbert et al. (2003)
Minimum net reproductive output	r_{min}	0	
Maximum net reproductive output	r_{max}	1 (2.9)	
Net reproductive output slope	k_r	0.5	
Divorce rate	α	0.04	Bried and Jouventin (2002)
Divorce mean pair quality	β	1	
Divorce pair quality difference	γ	1	
Juvenile transition probability	$\tau_{J\rightarrow I}$	0.2 (1)	Cuthbert et al. (2003)
Immature transition probability	$\tau_{I\rightarrow A}$	0.213 (0.5)	Cuthbert et al. (2003)
Divorced adult transition probability	$\tau_{D\rightarrow A}$	0.5	
Offspring density location	–	0	
Offspring density scale	–	2	
Pair correlation	ρ	0	

Table 2.2: Life history trait estimates and default parameter values for the demographic model. Values in parenthesis denote modifications for the fast life history parameterisation.

and divorce cost) in turn for both fast and slow life history strategies. Non-focal divorce parameters were held at default values (Table 2.2). We calculated the asymptotic population growth rate to explore how interactions between quality assortative pairing and different components of divorce influence population dynamics. Further, we explored the influence of divorce on demographic structure, specifically the stable distribution of breeding pairs across the pair quality spectrum, by calculating the pair distribution across a range of mean pair quality and pair quality difference parameters. We calculated population growth rate to examine the population-level consequences of any resulting variation in demographic structure.

2.2.5 Transient analysis

We explored how pairing and divorce parameters influence transient (short-term) responses to changes to population structure. We calculated transient metrics for both fast and slow life history strategies while varying correlation in pair quality in combination with underlying divorce parameters (baseline divorce rate, influence of mean pair quality, influence of pair quality difference). Transient metrics quantify the relative increase or decrease in population size after perturbation, both during transient fluctuations and after the population size has stabilised. Amplification is a measure of the maximum bounds on population size after perturbation. *First time step amplification* measures the largest increase in population size in the initial time step, *maximum amplification* records the largest population size during transient fluctuations, and *amplified inertia* indicates the long-term maximum relative to the original size of the perturbed population. Equivalent attenuation metrics represent the lowest bounds on the population size following perturbation. The bounds on the relative population size during and after transient adjustments indicate the sensitivity of a population to perturbations and how likely it is to be affected positively or negatively when perturbed (Stott et al. 2011). For example, if the amplified inertia is negative this indicates an overall reduction in population size in response to perturbation. The magnitude of transient responses is assessed relative to the original population size.

To generate the transient metrics for each life history parameter set, we calibrated the model to obtain $\lambda \approx 1$ by adjusting the slope of the survival (2.5) and recruitment (2.11) functions with respect to individual and pair quality, respectively. Using the resulting stationary parameterisation, we calculated the stable stage distribution, which indicates the proportion of the population in different life stages when the population is in a stable state. We altered the population structure from this stable state by making proportional adjustments to the five different life stages (juvenile, immature, adult and divorced individuals, and pairs) in combination, adjusting the size of each to 0, 0.5 or 1.0 of the amount in the stable stage distribution, resulting in a set of 243 possible combinations of perturbed stages. Using each of these combinations as a starting point, we projected the population for 100 time steps and calculated the first time step, minimum, maximum and long-term population size. After scaling these values by the initial population size, we recorded the first time step, maximum, and long-term amplification and attenuation across the set of perturbations. These metrics form the transient bounds of the population's response to perturbations (Stott et al. 2011).

2.3 Results

2.3.1 Influence of pairing and divorce on long-term population dynamics

Correlation in pair quality can buffer the impact of divorce

Population growth rate showed low sensitivity to baseline divorce rate, decreasing by up to 2% in populations with a slow life history as divorce rate increased (Fig. 2.4a). When pairs were more closely matched in quality the decrease in population growth rate was less marked and this pattern was similar between the fast and slow life history strategy (Figs 2.4a and 2.4e). We assumed in our model that reproduction is highest and the probability of divorce lowest when pairs have high mean pair quality (Equation 2.11, Fig. 2.3). Against these assumptions, increasing pair correlation, which leads to more high mean quality pairs, may contribute to further decreasing the negative impact of divorce on population growth rate.

We found that population growth rate was sensitive to the mean pair quality parameter when this parameter was close to zero (Figs 2.4b and 2.4f). Population growth rate increased sharply as the strength of the mean pair quality parameter increased from zero. Population growth rate recovered more rapidly as the mean pair quality parameter increased under a fast life history and when pairs were highly correlated. This result reflects a switch from a divorce function that is dominated by the quadratic pair quality difference term (Equation 2.8), with high divorce rates across the pair quality spectrum (Fig. 2.3c), to a function in which the influence of mean pair quality reduces the probability of divorce across the population (Fig. 2.3b).

Increasing the strength of the pair quality difference aspect of divorce had little influence on population growth rate in both slow and fast life histories (Figs 2.4c and 2.4g). As the strength of the pair quality difference parameter increased there was a slight negative impact (less than 1%) on population growth rate. This negative impact was strongest when pair correlation was low.

Varying the cost of divorce by changing the rate at which divorced individuals rejoin the pairing pool had little impact on population growth rate (Figs 2.4d and 2.4h). Even at the highest cost (no return of divorced individuals to the breeding pool) the impact on population growth rate was negligible, with much less than 1% difference in population

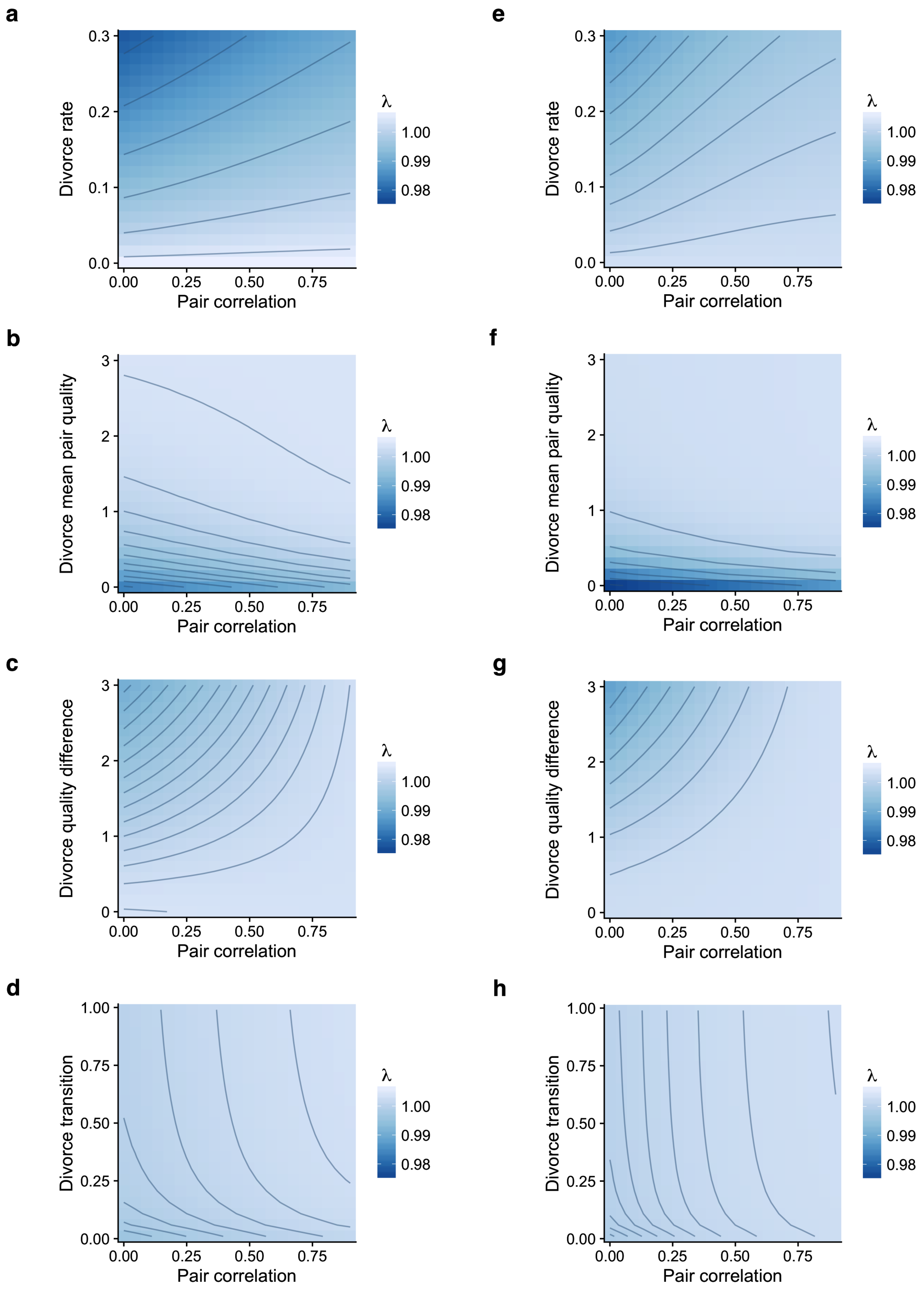

Figure 2.4: Population growth rate, λ, over a range of values for pair correlation and (a,e) baseline divorce rate; (b,f) influence of mean pair quality on divorce; (c,g) influence of quality difference on divorce; (d,h) transition rate of divorced individuals, under (a,b,c,d) slow life history and (e,f,g,h) fast life history.

growth rate across the range of pair correlation.

Pair quality aspects of divorce have little influence on long-term dynamics

The stable distribution of pairs was not strongly influenced by the relationship between pair quality and divorce (Fig. 2.5). As the sensitivity of divorce to differences in quality between pair members increased, the distribution of pairs became more concentrated along the line of equal quality, and this was particularly noticeable when divorce did not depend on mean pair quality ($\beta = 0$). There was a corresponding decrease in population growth rate when divorce was dominated by differences in pair quality, particularly under a fast life history (Figs 2.6a and 2.6b). However, the impact of the pair quality difference parameter on both pair quality distribution and population growth rate became negligible with increasing sensitivity of divorce to mean pair quality.

2.3.2 Transient population responses to pairing and divorce

Pairing and divorce dynamics have most impact on transient amplification

Maximum amplification (Fig. 2.7) and amplified inertia (Fig. 2.8) showed the greatest sensitivity to variation in pairing and divorce parameters. These amplification metrics responded strongly to changes in divorce parameters, changing by 0.5–2 times the population size as divorce parameters were varied (Figs 2.7 and 2.8). Although these metrics responded strongly to variation in divorce parameters for both fast and slow life history strategies, the magnitude of responses tended to be greater under a fast life history compared to a slow life history. It is notable that amplified inertia was negative for slow life history for a number of different combinations of pairing and divorce parameters (Fig. 2.8). That is, despite potential increases in population size during transient fluctuations, the population decreased in size in the long term. Our results suggest that when divorce rates are high, slow life history populations may be more sensitive to perturbations than populations with a fast life history.

The only other transient metrics to show any response to pairing and divorce parameters were maximum attenuation (Fig. S2.1, Supporting information) and attenuated inertia (Fig. S2.2, Supporting information), with responses of up to half the initial population size to changes in divorce rate and the other divorce parameters in slow, but not fast, life history. Our results show that divorce can influence the minimum bound on population size after

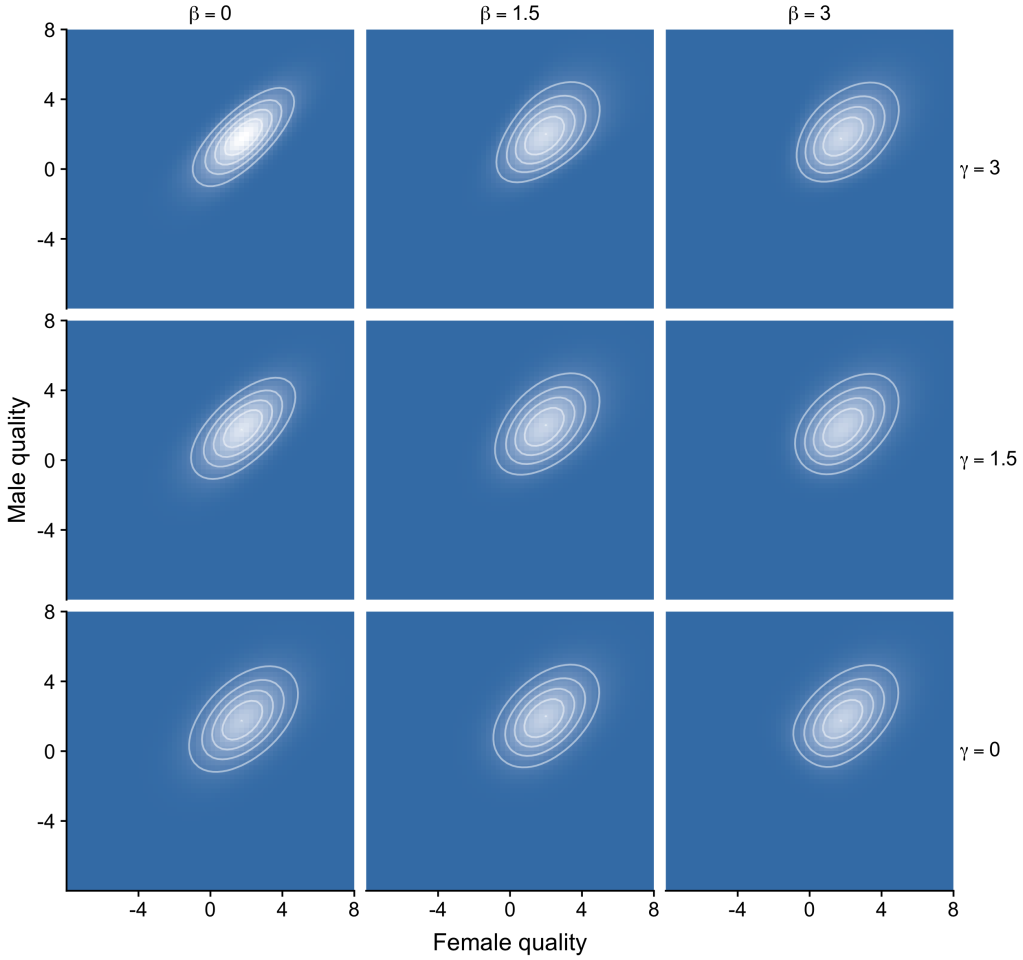

Figure 2.5: Pair quality distribution over a range of values for the influence of mean pair quality, β, and quality difference, γ, on divorce.

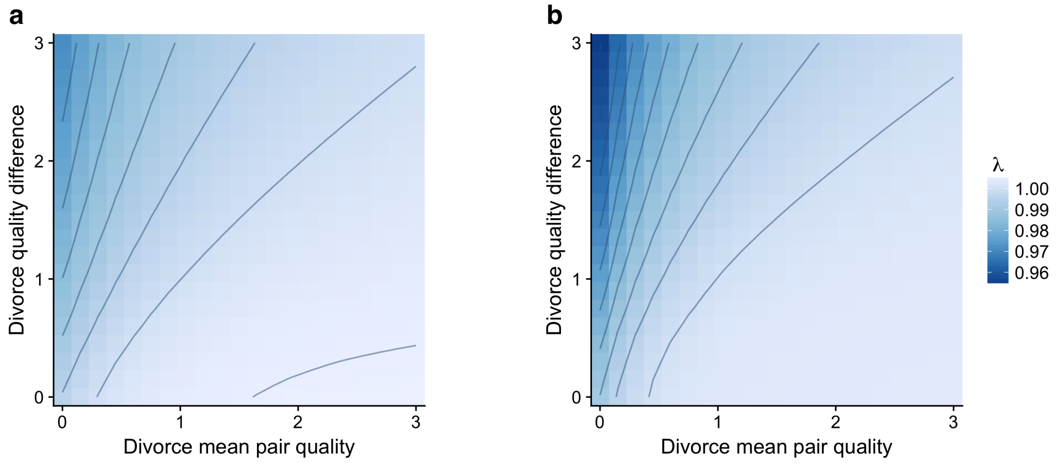

Figure 2.6: Population growth rate, λ, over a range of values for the influence of mean pair quality and quality difference on divorce, under (a) slow life history and (b) fast life history.

perturbation, but that this effect is slight and apparent only for slow-lived species. Slow life history populations are subject to less attenuation when divorce rates are lower, indicating greater resilience to perturbations.

Low levels of interaction between pairing and divorce in transient responses

While amplification metrics responded to some extent to variation in divorce parameters and pair correlation, the effect of pairing on amplified inertia did not change across different levels of baseline divorce rate (Fig. 2.8). However, low levels of interaction between pair correlation and the other divorce parameters influenced both maximum amplification and amplified inertia (Figs 2.7 and 2.8). These patterns can be attributed to the influence of pair quality difference on the probability of divorce in our model formulation. Increasing pair correlation reduces differences in quality among pairs and so decreases the overall incidence of divorce, since better matched pairs have a lower probability of divorce. Pair correlation has an impact on transient bounds when the influence of divorce quality difference is strong in comparison to the influence of mean pair quality (for example, at low values of the mean pair quality parameter or at high values of the pair quality difference parameter).

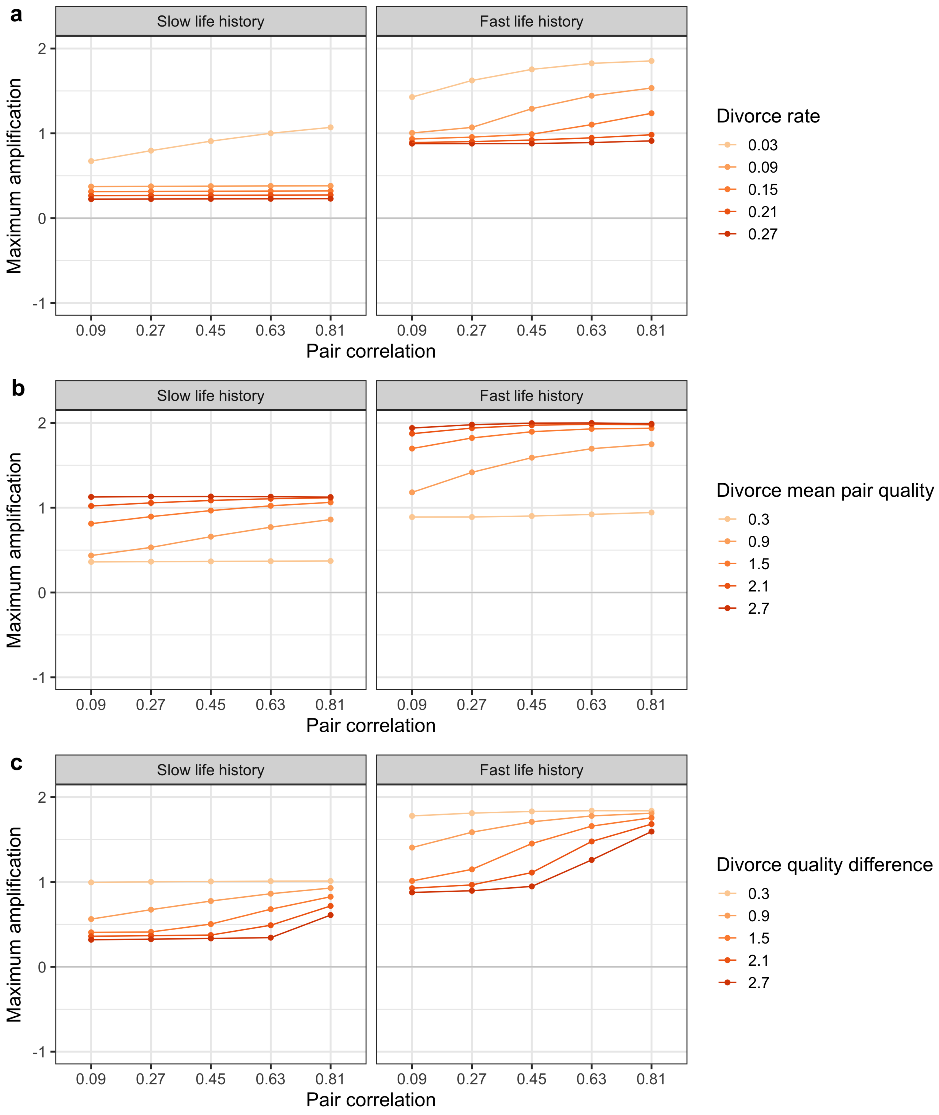

Figure 2.7: Maximum amplification plotted against strength of pair correlation under slow and fast life histories, varying (a) baseline divorce rate, (b) influence of mean pair quality on divorce and (c) influence of pair quality difference on divorce.

2.4 Discussion

While there have been numerous models crafted to explore pairing and divorce, many have focused on frequency-dependent dynamics (e.g. Legendre et al. 1999, Maxin and Berec 2010, Jenouvrier et al. 2010, Schindler et al. 2013, Shyu and Caswell 2018) and very few have been explicit for pair quality (but see McNamara and Forslund 1996, Johnstone 1997, McNamara et al. 1999, for game theoretic approaches that consider individual quality). Here, we implemented classical sensitivity analyses, the cornerstone of modern conservation biology,

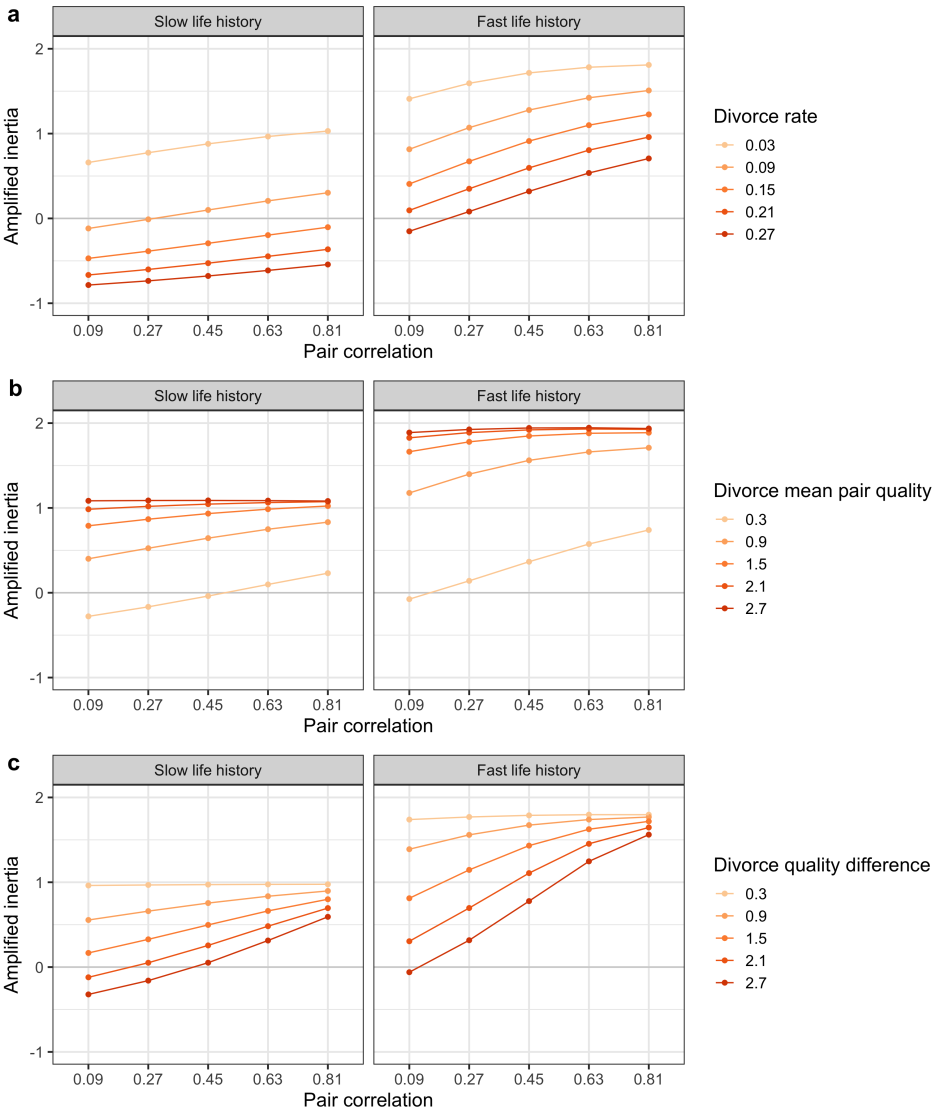

Figure 2.8: Amplified inertia plotted against strength of pair correlation under slow and fast life histories, varying (a) baseline divorce rate, (b) influence of mean pair quality on divorce and (c) influence of pair quality difference on divorce.

in a symmetric demographic framework with an explicit representation of individual quality. Our objective was to investigate the sensitivity of asymptotic population growth rate to quality-linked pairing and divorce processes in a demographic conservation framework. We used symmetric demography to suppress the nonlinear components of elasticities which arise due to frequency dependence (Caswell 2008, Haridas et al. 2014), allowing us to focus on classical sensitivities. In addition to this classical approach, we used emerging tools for the analysis of transient dynamics, which can reveal important short- versus long-term responses to perturbations. The sensitivity of population growth rate and transient dynamics

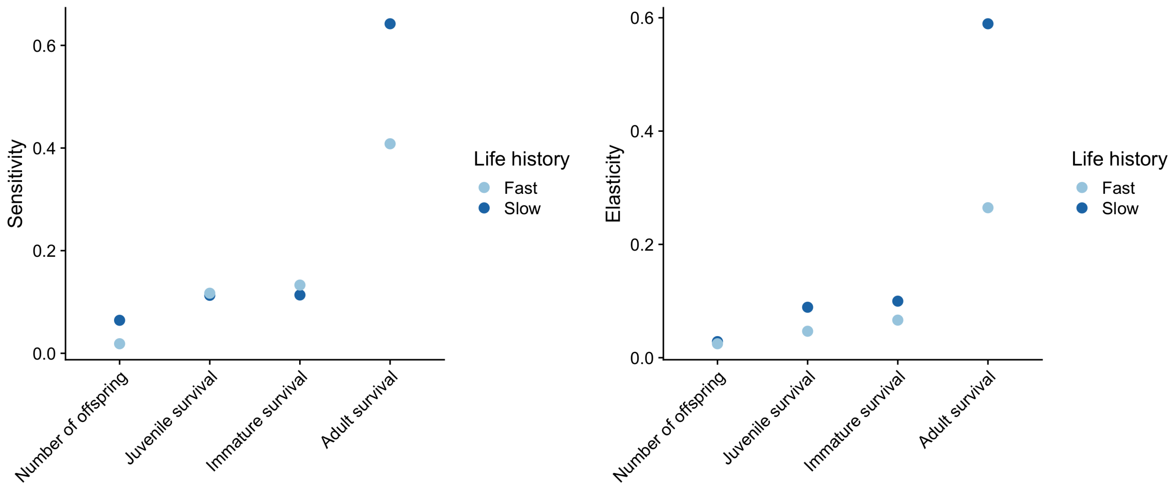

Figure 2.9: Sensitivity and elasticity of population growth rate to reproduction and survival parameters.

are important considerations when developing conservation strategies (Caswell 2000, Stott et al. 2012). In the following sections we review our core results then explore several assumptions in our model that might influence our findings and offer future research opportunities.

2.4.1 Divorce and asymptotic population growth rate

We found that the sensitivity of population growth rate to most pairing and divorce parameters was low (Fig. 2.4). It is well-established in classical demography that adult survival is the most sensitive part of long-lived species' life cycle; small changes in adult survival have the greatest influence on population growth rate (Fig. 2.9; Sæther and Bakke 2000). This suggests that the sensitivity of population growth rate to changes in divorce and pairing will be weak unless these processes are tightly linked to adult survival. The evidence, however, for an impact of divorce on survival is limited (Heg et al. 2003, Nicolai et al. 2012, Culina et al. 2015b, Jankowiak et al. 2018), so we assumed that divorce incurred a cost to reproduction through a penalty on time to repairing, but had no impact on survival. Under this assumption, any impacts of divorce on population growth reflect the reduction in reproductive output due to delayed repairing. However, the sensitivity and elasticity of population growth rate to the number of offspring was low under both model parameterisations (Fig. 2.9), so it is unsurprising that changes in pairing and divorce parameters had relatively little effect on population growth rate. As noted above, unless there is a strong link between pairing and

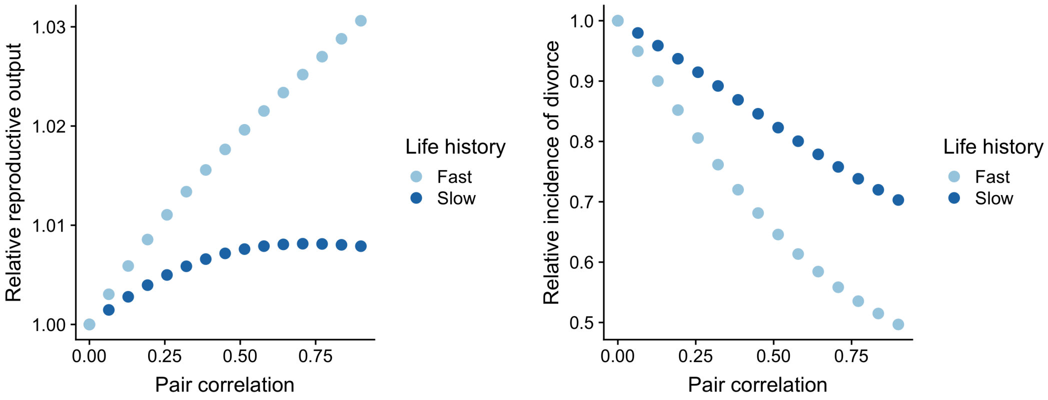

Figure 2.10: Relative reproductive output and relative incidence of divorce across the stable pair distribution in relation to strength of pair correlation and life history.

divorce parameters and survival, it is unlikely that changes in these parameters would have a large influence on population growth rate. However, even if there are no direct effects of divorce or delayed pairing on survival, the combination of pair quality, divorce, timing of pairing and re-pairing may interact nonlinearly to influence population growth rate.

A closer look at the small effects of pairing and divorce on population growth rate reveal two aspects to which population growth rate showed some sensitivity. Firstly, the impact of divorce on population growth rate was lower when pairs were more closely matched in quality (Figs 2.4a and 2.4e). Fig. 2.10 shows the relative reproductive output and incidence of divorce across pairs in the stable distribution plotted against pair correlation for both fast and slow life histories. As pairs become more strongly matched, the reproductive output increases and the incidence of divorce decreases. The increase in offspring recruitment and reduction of costly delays to repairing associated with divorce may provide a mechanism for increased pair correlation to reduce the impact of divorce on population growth rate. However, since this mechanism acts through reproduction, which has low sensitivity, the effect is not strong. Despite a stronger increase in relative reproductive output and a sharper decrease in the relative incidence of divorce with increasing pair correlation under a fast life history strategy (Fig. 2.10), we found little difference in the sensitivity of population growth rate to the degree of assortative pairing under the alternative life histories.

Secondly, population growth rate was sensitive to the form of the divorce function, decreasing sharply when the mean pair quality parameter was close to zero, particularly for the fast life history strategy (Figs 2.4b and 2.4f, Fig. 2.6). In our formulation of the divorce function, when the parameter for difference in pair quality becomes dominant (as is the case when the mean pair quality parameter is close to zero) there is a high probability of divorce across the pair quality spectrum (Fig. 2.3c). This result suggests that the impact of an increasing incidence of divorce, characterised in the model as a reproductive cost, may depend on the relative importance of recruitment in the alternate life history strategies. However, this is contradicted by the fact that the impact of baseline divorce was strongest in the slow life history scenario (Fig. 2.4a), indicating that the divorce function effect does not simply correspond to increasing the overall incidence of divorce. Moreover, the elasticity of population growth rate to reproduction was similar in the fast and slow life history parameterisations (Fig. 2.9).

Across both of these small effects, increased pair correlation, which results in pairs being more closely matched and so less likely to divorce, mitigated the impacts of divorce slightly. In the context of a frequency-dependent pairing model, Schindler et al. (2013) found that size-assortative pairing had a slight (of the order of 10^{-4}) influence on population growth rate, but found that a positive increase in population growth rate was associated with disassortative or sexually selected mating rather than assortative mating. As well as being frequency-dependent, the model of Schindler et al. (2013) does not include divorce so the results are not directly comparable.

2.4.2 Transient responses to divorce

Several recent studies have identified a range of metrics of short-term transient dynamics that are potentially important for conservation and that can be obtained from matrix and integral projection models (Stott et al. 2011, Horvitz et al. 2018). They include metrics that highlight large or small population size changes (amplitude), their frequency (cycles) and inertia (persistence) in short time windows after a perturbation. Given the time frames over which conservation planning is typically generated and implemented and over which habitat loss or extreme events impact populations, these metrics are valuable in predicting outcomes of interventions (Ezard et al. 2010). Furthermore, these metrics may have magnitudes that are quite different to long-term responses in long-lived species (Koons et al. 2005). As the sensitivity of long-term population growth rate to divorce and pairing parameters is relatively low in our model, an exploration of transient responses may help to understand over what time scale conservation planning needs to consider these types of variables.

The amplification metrics varied most in response to changes in pairing and divorce parameters, particularly those measuring maximum short-term population size (maximum amplification) and the persistence of short-term increases in population size (amplified inertia). The patterns of the transient responses suggest that short-term population recovery may be influenced by pairing and divorce processes. For example, the bounds of the transient envelope move down as baseline divorce rate increases, but increasing pair correlation shifts the bounds up (e.g. Fig. 2.8a and Fig. S2.2a), indicating that quality-matched pairing can buffer the impact of divorce.

While patterns of transient responses were similar across life histories, the absolute values of the transient bounds under a fast life history were up to double the values under a slow life history, suggesting that a slower life history strategy is less responsive to perturbations. However, under a slow life history the amplified inertia was negative for some pairing and divorce parameter combinations, indicating that slow life history populations are more likely to be negatively affected by perturbations when divorce rates are high. The minimum short-term population size (maximum attenuation) and the persistence of short-term decreases in population size (attenuated inertia) were somewhat responsive to pairing and divorce parameters in slow life histories but showed little sensitivity in fast life histories. Apart from the responses in amplification and attenuation described above, the transient dynamics, as measured by these metrics, were largely insensitive to variation in pair quality and divorce under our model formulation.

Contrary to what we saw in our analysis of long-term population growth rate, we found that certain metrics (e.g. amplified inertia) were similarly responsive across pairing and divorce parameters, and across life history strategies, although the magnitude of responses differed between life histories. Other metrics (e.g. attenuated inertia) showed similar responses to changes in pairing and divorce parameters but only responded strongly to these parameters in the slow life history strategy. The sensitivity of transient amplitudes indicates that even relatively small changes in aspects of pairing and divorce can impact on short-term population responses. Amplified inertia, the long-term maximum bound on population size relative to the initial population size, is of particular concern in a conservation setting, since it indicates the maximum size at which the population stabilises relative to the original size after disturbance or intervention. Hence, this metric indicates whether an increase in population size after disturbance is possible (positive value) or not (negative value). For some combinations of pairing and divorce parameters the transient metrics predict a decrease in population size in response to perturbations.

2.4.3 Model assumptions with consequences for pairing and divorce dynamics

Several assumptions underlying our model limit its ability to capture both the long-term and transient dynamics of the system. Firstly, we have assumed that divorce incurs a cost to reproduction but we have not explored alternative divorce costs. Secondly, we depend on demographic symmetry and a large population size to be able to disregard frequency dependence and demographic stochasticity. Finally, our model does not incorporate density dependence. In the following sections we explore the implications of these assumptions.

Alternative costs of divorce

We have assumed a cost of divorce on reproductive output by imposing a delay on the transition of a divorced individual to the pairing pool, resulting in the loss of one or more reproductive opportunities (Culina et al. 2015c). Divorce could be costly in other ways and under different costs the consequences of divorce may deviate from the present results. An alternative reproductive cost of divorce would be a direct reduction in reproductive success following divorce, which could arise, for example, due to lack of familiarity with a new mate (Ens et al. 1996, Culina et al. 2015c). However, whether the divorce cost manifested as a lost breeding opportunity or reduced reproductive success following divorce, the outcome would be an initial reduction in reproductive output, so we would not expect to see a large difference in the impact of these alternative formulations. Furthermore, the sensitivity of population growth rate to reproduction is low (Fig. 2.9), so any direct reproductive costs of divorce would need to be very large to influence population performance. In contrast, empirical evidence points to divorce being an adaptive strategy that results in individuals improving reproductive success (Culina et al. 2015c), although some studies have noted a temporary reduction in breeding success following divorce (Ens et al. 1993, 1996) or changes in breeding success which are dependent on the status of individuals after divorce (Heg et al. 2003, Jeschke et al. 2007).

Divorce may influence other aspects of fitness, in particular survival (Culina et al. 2015c). There may be direct effects of divorce or delayed pairing on survival, for example due to risks involved in mate search (Nicolai et al. 2012), or the lower quality or condition of divorced individuals may make them more susceptible to death (Heg et al. 2003). Since population growth rate is most sensitive to survival (Fig. 2.9), such effects might be important in a conservation context. Survival benefits of pair fidelity have been demonstrated in Paridae (Culina et al. 2013, 2015b) and in European blackbirds (Jankowiak et al. 2018). However, the detailed individual capture histories and pairing information required to determine the effect of divorce on survival mean that further support for increased mortality following divorce is limited to indirect evidence of increased mortality risk following partner loss, for example due to predation or harvesting (Nicolai et al. 2012). It is clear, though, that if divorced individuals were more likely to die we would expect a reduction in the long-term rate of population increase, because of the high sensitivity of population growth rate to survival in long-lived species. We would also expect to see a negative effect on transient dynamics, with populations being slower to recover from perturbations due to the loss of individuals with reproductive potential and with transient amplification of population size likely to be reduced, particularly at higher levels of divorce. Survival costs of divorce could be explored by including a survival penalty for individuals in the divorced state.

Demographic stochasticity, Allee effects and divorce

Our modelling framework depends on population size being large enough that demographic stochasticity, that is, random variation in mortality and birth at an individual level, can be disregarded. This allows us to implement a symmetric pairing model which captures the within-pair correlation that arises when individuals seek a partner with a similar quality to their own (Johnstone 1997). Demographic stochasticity can drive variation in sex ratio and lead to mate limitation, with negative consequences for individual fecundity (Engen et al. 2003, Bessa-Gomes et al. 2004). Fluctuations in the sex ratio produce a type of component Allee effect, which, if it is not offset by other factors, may contribute to a demographic Allee effect (Stephens et al. 1999, Gascoigne et al. 2009). Component Allee effects arising from fluctuations in the sex ratio can occur across mating systems, including monogamy (Engen et al. 2003, Bessa-Gomes et al. 2004), although they may be buffered by population processes such as interactions between operational sex ratios and mating rates (Bessa-Gomes et al. 2004). While there is some empirical evidence for component Allee effects, cases in which they have been shown to contribute to demographic Allee effects remain small in number (Gascoigne et al. 2009). It is important to note that Allee effects due to sex ratio fluctuations may only manifest strongly in species where sex ratio effects are aligned with the vital rates to which population growth rate is most sensitive. If the sensitivity of population growth rate to reproduction is low, component Allee effects with a negative impact on fecundity may have only minor consequences for a population.

Fluctuations in the sex ratio could affect populations when divorce occurs. If the operational sex ratio is skewed, then divorced individuals may be unable to find a partner, resulting in missed breeding opportunities. Moreover, in the context of individual quality-based pairing, lack of mates of a similar quality under limiting population size would increase the number of poorly matched pairs, again potentially depressing the population's reproductive output. These outcomes could increase the reproductive costs of divorce. But, as noted previously, we would not expect to see a strong effect on population growth rate as a result of variation in fecundity in long-lived species because population growth rate has lower elasticity to fecundity than survival. However, if mate-finding were costly in terms of survival then mate limitation would be expected to have a negative impact on population growth rate.

Mate-finding Allee effects remain a concern, particularly in areas such as conservation management or invasive species control, where fates of populations at low density are of key importance (Stephens and Sutherland 1999). Selective harvesting can result in skewed operational sex ratios with significant impacts on population viability (Ginsberg and Milner-Gulland 1994, Milner-Gulland et al. 2003). However, the consequences of skewed sex ratio depend on the sensitivity of population growth rate to the affected rates. Despite substantial reduction in fecundity due to female-biased bycatch mortality in wandering albatross, *Diomedea exulans*, impacts on annual population growth rates were relatively slight, although the associated change in demographic structure may have had longer term consequences (Mills and Ryan 2005).

Density dependence and divorce

In natural populations, density-dependent processes moderate population growth rate, for example through effects on survival and reproduction (e.g. Larsson and Forslund 1994, Frederiksen and Bregnballe 2000, Paradis et al. 2002). In the absence of perturbations, we expect populations under density-dependent regulation to be close to equilibrium and to have a population growth rate around 1. Ignoring density dependence can produce an unrealistic picture of long-term population trends, since vital rates for such populations are subject to density-dependent feedback (Freckleton et al. 2003). Furthermore, in the presence of density dependence, alternative interpretation and calculation of sensitivities and elasticities is required because population growth rate tends to remain stable through density-dependent regulation (Caswell 2008).

There are suggestions but limited empirical evidence that the density of conspecifics may influence divorce rates (Dubois et al. 1998, Kokko and Rankin 2006, Maxin and Berec 2010, Culina et al. 2015a). Kokko and Rankin (2006) suggest that population density influences the frequency of encountering potential partners and hence alters the costs and benefits of divorce, so that we should expect divorce rate to be positively correlated with population density. If a lack of potential partners in low density populations resulted in lower divorce rates, this could operate as a feedback mechanism to regulate population growth and counteract Allee effects (Kokko and Rankin 2006). Furthermore, population density may affect levels of competitive interactions which lead to divorce (Jeschke et al. 2007). While social environment has been found to influence the probability of divorce (Culina et al. 2015a), there is no clear evidence that coloniality (i.e. high population density) enhances the adaptive potential of divorce (Culina et al. 2015c), perhaps due to heterogeneity of outcomes for divorcing individuals (Heg et al. 2003, Jeschke et al. 2007).

In the context of our question about the sensitivity of population growth to pairing and divorce, we suggest that interactions between population density and divorce are unlikely to have a strong influence on density-dependent populations. Whether divorce costs manifest as a cost of reproduction (it takes longer to find a mate) or survival (mate search increases mortality risk), an increase in divorce rate at high population density would produce similar effects to those expected under compensatory density regulation (i.e. increased competition for resources leading to reduced survival and/or reproductive output). Hence, if divorce were positively associated with population density, it would act to strengthen any density-dependent feedbacks. While our analysis showed that divorce rate can have a small effect on population growth rate, the effect was not strong under our model formulation, in which divorce only imposes a cost to reproduction. Our results suggest that, for long-lived monogamous birds, divorce will have only a minimal effect on the regulation of high density populations, unless divorce results in lower adult survival at high population density.

2.4.4 Conclusions

This study has explored the population-level consequences of pairing and divorce processes in long-lived monogamous birds through the sensitivity and transient dynamics of population growth rate. Under the constraints of our model, we have seen that both long-term and short-term dynamics are largely insensitive to the pairing process, pair quality and divorce. These patterns were mirrored across alternative life history strategies corresponding to generally long-lived monogamous species. We suggest that the insensitivity of population growth rate to pairing and divorce results from assuming that the cost of divorce takes the form of a loss of reproductive output, because the elasticity of population growth rate to reproduction is low in long-lived species. As discussed above, we would not expect to see very different outcomes unless divorce cost was strongly linked to survival. However, although there is good evidence for divorce being linked to changes in reproductive output, empirical evidence for a mortality cost of divorce is lacking. The impact of pairing and divorce dynamics on population growth rate and transient dynamics is likely to be minimal in long-lived monogamous species, as long as divorce costs are reflected in reproduction and have low impact on survival. Other processes, such as those affecting adult survival, are likely to be more important in the conservation management of long-lived monogamous species.

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2.6 Author contributions

T.D.J., D.Z.C. and A.P.B. conceived and designed the study. T.D.J. implemented the model, carried out the analysis and led the writing of the manuscript. D.Z.C. and A.P.B. contributed critically to the drafts and gave final approval for publication.

2.7 References

Aubry LM, Cam E, Koons DN, Monnat JY, Pavard S. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology*, **80**(2), 375–383.

Berec L, Boukal DS. 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. *Oikos*, **104**(1), 122–132.

Bergeron P, Baeta R, Pelletier F, Réale D, Garant D. 2011. Individual quality: tautology or biological reality? *Journal of Animal Ecology*, **80**(2), 361–364.

Bessa-Gomes C, Legendre S, Clobert J. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters*, **7**(9), 802–812.

Black J, ed.. 1996. *Partnership in birds*. Oxford University Press, Oxford.

Bried J, Jouventin P. 2002. Site and mate choice in seabirds: an evolutionary approach. In Schreiber EA, Burger J, eds., *Biology of marine birds*, pp. 263–305. CRC press.

Cam E, Link WA, Cooch EG, Monnat JY, Danchin E, Travis EJ. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *The American Naturalist*, **159**(1), 96–105.

Caswell H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**(3), 619–627.

Caswell H. 2008. Perturbation analysis of nonlinear matrix population models. *Demographic Research*, **18**, 59–116.

Caswell H, Weeks DE. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. *The American Naturalist*, **128**(5), 707–735.

Childs DZ, Sheldon BC, Rees M. 2016. The evolution of labile traits in sex- and age-structured populations. *Journal of Animal Ecology*, **85**(2), 329–342.

Coulson T, Kendall BE, Barthold J, Plard F, Schindler S, Ozgul A, Gaillard JM. 2017. Modeling adaptive and nonadaptive responses of populations to environmental change. *The American Naturalist*, **190**(3), 313–336.

Culina A, Hinde CA, Sheldon BC. 2015a. Carry-over effects of the social environment on future divorce probability in a wild bird population. *Proc. R. Soc. B*, **282**(1817), 20150920.

Culina A, Lachish S, Pradel R, Choquet R, Sheldon BC. 2013. A multievent approach to estimating pair fidelity and heterogeneity in state transitions. *Ecology and Evolution*, **3**(13), 4326–4338.

Culina A, Lachish S, Sheldon BC. 2015b. Evidence of a link between survival and pair fidelity across multiple tit populations. *Journal of Avian Biology*, **46**(5), 507–515.

Culina A, Radersma R, Sheldon BC. 2015c. Trading up: the fitness consequences of divorce in monogamous birds. *Biological Reviews*, **90**(4), 1015–1034.

Cuthbert R, Ryan PG, Cooper J, Hilton G. 2003. Demography and population trends of the Atlantic yellow-nosed albatross. *The Condor*, **105**(3), 439–452.

Dubois F, Cézilly F. 2002. Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*, **52**(5), 357–364.

Dubois F, Cézilly F, Pagel M. 1998. Mate fidelity and coloniality in waterbirds: a comparative analysis. *Oecologia*, **116**(3), 433–440.

Easterling MR, Ellner SP, Dixon PM. 2000. Size-specific sensitivity: applying a new structured population model. *Ecology*, **81**(3), 694–708.

Engen S, Lande R, Sæther BE. 2003. Demographic stochasticity and allee effects in populations with two sexes. *Ecology*, **84**(9), 2378–2386.

Ens BJ, Choudhury Sharmila C, Black JM. 1996. Mate fidelity and divorce in monogamous birds. In Black JM, ed., *Partnerships in Birds: The Study of Monogamy*, p. 344. Oxford University Press, Oxford.

Ens BJ, Safriel UN, Harris MP. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour*, **45**(6), 1199–1217.

Ezard THG, Bullock JM, Dalgleish HJ, Millon A, Pelletier F, Ozgul A, Koons DN. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology*, **47**(3), 515–523.

Fay R, Barbraud C, Delord K, Weimerskirch H. 2016. Variation in the age of first reproduction: different strategies or individual quality? *Ecology*, **97**(7), 1842–1851.

Fay R, Barbraud C, Delord K, Weimerskirch H. 2017. From early life to senescence: individual heterogeneity in a long-lived seabird. *Ecological Monographs*, **88**(1), 60–73.

Fayet AL, Shoji A, Freeman R, Perrins CM, Guilford T. 2017. Within-pair similarity in migration route and female winter foraging effort predict pair breeding performance in a monogamous seabird. *Marine Ecology Progress Series*, **569**, 243–252.

Freckleton RP, Matos DMS, Bovi MLA, Watkinson AR. 2003. Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology*, **40**(5), 846–858.

Frederiksen M, Bregnballe T. 2000. Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. *Journal of Animal Ecology*, **69**, 737–752.

Gascoigne J, Berec L, Gregory S, Courchamp F. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology*, **51**(3), 355–372.

Gerber LR, White ER. 2014. Two-sex matrix models in assessing population viability: when do male dynamics matter? *Journal of Applied Ecology*, **51**(1), 270–278.

Ginsberg JR, Milner-Gulland EJ. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology*, **8**(1), 157–166.

Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, **78**(1), 143–151.

Haridas CV, Eager EA, Rebarber R, Tenhumberg B. 2014. Frequency-dependent population dynamics: effect of sex ratio and mating system on the elasticity of population growth rate. *Theoretical Population Biology*, **97**, 49–56.

Heg D, Bruinzeel LW, Ens BJ. 2003. Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. *Animal Behaviour*, **66**(1), 175–184.

Horvitz CC, Denslow JS, Johnson T, Gaoue O, Uowolo A. 2018. Unexplained variability among spatial replicates in transient elasticity: implications for evolutionary ecology and management of invasive species. *Population Ecology*, **60**(1), 61–75.

Ismar SMH, Daniel C, Stephenson BM, Hauber ME. 2009. Mate replacement entails a fitness cost for a socially monogamous seabird. *Naturwissenschaften*, **97**(1), 109–113.

Jankowiak Ł, Cholewa M, Wysocki D. 2018. Survival costs of within- and between-season mate change in the European blackbird *Turdus merula*. *Journal of Avian Biology*, **49**(6).

Jenouvrier S, Caswell H, Barbraud C, Weimerskirch H. 2010. Mating behavior, population growth, and the operational sex ratio: a periodic two-sex model approach. *The American Naturalist*, **175**(6), 739–752.

Jeschke JM, Kokko H. 2008. Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology*, **63**(1), 1–9.

Jeschke JM, Wanless S, Harris MP, Kokko H. 2007. How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce? *Behavioral Ecology*, **18**(2), 460–466.

Johnstone RA. 1997. The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology*, **40**(1), 51–59.

Kokko H, Jennions MD. 2008. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, **21**(4), 919–948.

Kokko H, Johnstone RA. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **357**(1419), 319–330.

Kokko H, Rankin DJ. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **361**(1466), 319–334.

Koons DN, Grand JB, Zinner B, Rockwell RF. 2005. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, **185**(2), 283–297.

Larsson K, Forslund P. 1994. Population dynamics of the barnacle goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. *Journal of Animal Ecology*, **63**, 954–962.

Lee AM, Sæther BE, Engen S, Eckert AECG, McPeek EMA. 2011. Demographic stochasticity, Allee effects, and extinction: the influence of mating system and sex ratio. *The American Naturalist*, **177**(3), 301–313.

Legendre S, Clobert J, Møller AP, Sorci G, Gotelli AENJ, Harrison S. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *The American Naturalist*, **153**(5), 449–463.

Lescroël A, Dugger KM, Ballard G, Ainley DG. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology*, **78**(4), 798–806.

Lewis S, Wanless S, Elston DA, Schultz MD, Mackley E, Du Toit M, Underhill JG, Harris MP. 2006. Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology*, **75**(6), 1304–1312.

Maxin D, Berec L. 2010. A two-sex demographic model with single-dependent divorce rate. *Journal of Theoretical Biology*, **265**(4), 647–656.

McNamara JM, Forslund P. 1996. Divorce rates in birds: predictions from an optimization model. *The American Naturalist*, **147**(4), 609–640.

McNamara JM, Forslund P, Lang A. 1999. An ESS model for divorce strategies in birds. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **354**(1380), 223–236.

Mills MSL, Ryan PG. 2005. Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Animal Conservation*, **8**(4), 359–367.

Milner-Gulland EJ, Bukreeva OM, Coulson T, Lushchekina AA, Kholodova MV, Bekenov AB, Grachev IA. 2003. Reproductive collapse in saiga antelope harems. *Nature*, **422**(6928), 135–135.

Moyes K, Morgan BJT, Morris A, Morris SJ, Clutton-Brock TH, Coulson T. 2009. Exploring individual quality in a wild population of red deer. *Journal of Animal Ecology*, **78**(2), 406–413.

Nicolai CA, Sedinger JS, Ward DH, Boyd WS. 2012. Mate loss affects survival but not breeding in black brant geese. *Behavioral Ecology*, **23**(3), 643–648.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD. 2002. Exploring density-dependent relationships in demographic parameters in populations of birds at a large spatial scale. *Oikos*, **97**, 293–307.

Parker G. 1983. Mate quality and mating decisions. *Mate choice*, pp. 141–166.

Petry WK. 2016. *Population and community consequences of ecological differences between the sexes*. Ph.D. thesis, UC Irvine.

Pollard JH. 1997. Modelling the interaction between the sexes. *Mathematical and Computer Modelling*, **26**(6), 11–24.

Rowley I. 1983. Re-mating in birds. In Bateson PPG, ed., *Mate choice*, pp. 331–360. Cambridge University Press.

Sæther BE, Bakke Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**(3), 642–653.

Sæther BE, Engen S, Lande R, Møller AP, Bensch S, Hasselquist D, Beier J, Leisler B. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *Journal of Animal Ecology*, **73**(5), 925–934.

Schindler S, Gaillard JM, Grüning A, Neuhaus P, Traill LW, Tuljapurkar S, Coulson T. 2015. Sex-specific demography and generalization of the Trivers-Willard theory. *Nature*, **526**(7572), 249–252.

Schindler S, Neuhaus P, Gaillard JM, Coulson T. 2013. The influence of nonrandom mating on population growth. *The American Naturalist*, **182**(1), 28–41.

Schreiber EA, Burger J. 2001. *Biology of Marine Birds*. CRC marine biology. CRC Press.

Shelton AO, West AES, DeAngelis EDL. 2010. The ecological and evolutionary drivers of female-biased sex ratios: two-sex models of perennial seagrasses. *The American Naturalist*, **175**(3), 302–315.

Shyu E, Caswell H. 2016. A demographic model for sex ratio evolution and the effects of sex-biased offspring costs. *Ecology and Evolution*, **6**(5), 1470–1492.

Shyu E, Caswell H. 2018. Mating, births, and transitions: a flexible two-sex matrix model for evolutionary demography. *Population Ecology*, pp. 1–16.

Snyder KT, Freidenfelds NA, Miller TEX. 2014. Consequences of sex-selective harvesting and harvest refuges in experimental meta-populations. *Oikos*, **123**(3), 309–314.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**(2), 173–187.

Stephens PA, Frey-roos F, Arnold W, Sutherland WJ. 2002. Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology*, **71**(2), 343–361.

Stephens PA, Sutherland WJ. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution*, **14**(10), 401–405.

Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is the Allee effect? *Oikos*, **87**(1), 185–190.

Stott I, Hodgson DJ, Townley S. 2012. Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. *Methods in Ecology and Evolution*, **3**(4), 673–684.

Stott I, Townley S, Hodgson DJ. 2011. A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, **14**(9), 959–970.

Traill LW, Schindler S, Coulson T. 2014. Demography, not inheritance, drives phenotypic change in hunted bighorn sheep. *Proceedings of the National Academy of Sciences*, **111**(36), 13223–13228.

Tsai WP, Sun CL, Punt AE, Liu KM. 2014. Demographic analysis of the shortfin mako shark, *Isurus oxyrinchus*, in the Northwest Pacific using a two-sex stage-based matrix model. *ICES Journal of Marine Science: Journal du Conseil*, **71**(7), 1604–1618.

Veran S, Beissinger SR. 2009. Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters*, **12**(2), 129–143.

Weladji RB, Loison A, Gaillard JM, Holand Ø, Mysterud A, Yoccoz NG, Nieminen M, Stenseth NC. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, **156**(1), 237–247.

Wilson AJ, Nussey DH. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, **25**(4), 207–214.

Zhang H, Vedder O, Becker PH, Bouwhuis S. 2015. Contrasting between- and within-individual trait effects on mortality risk in a long-lived seabird. *Ecology*, **96**(1), 71–79.

2.8 Supporting information

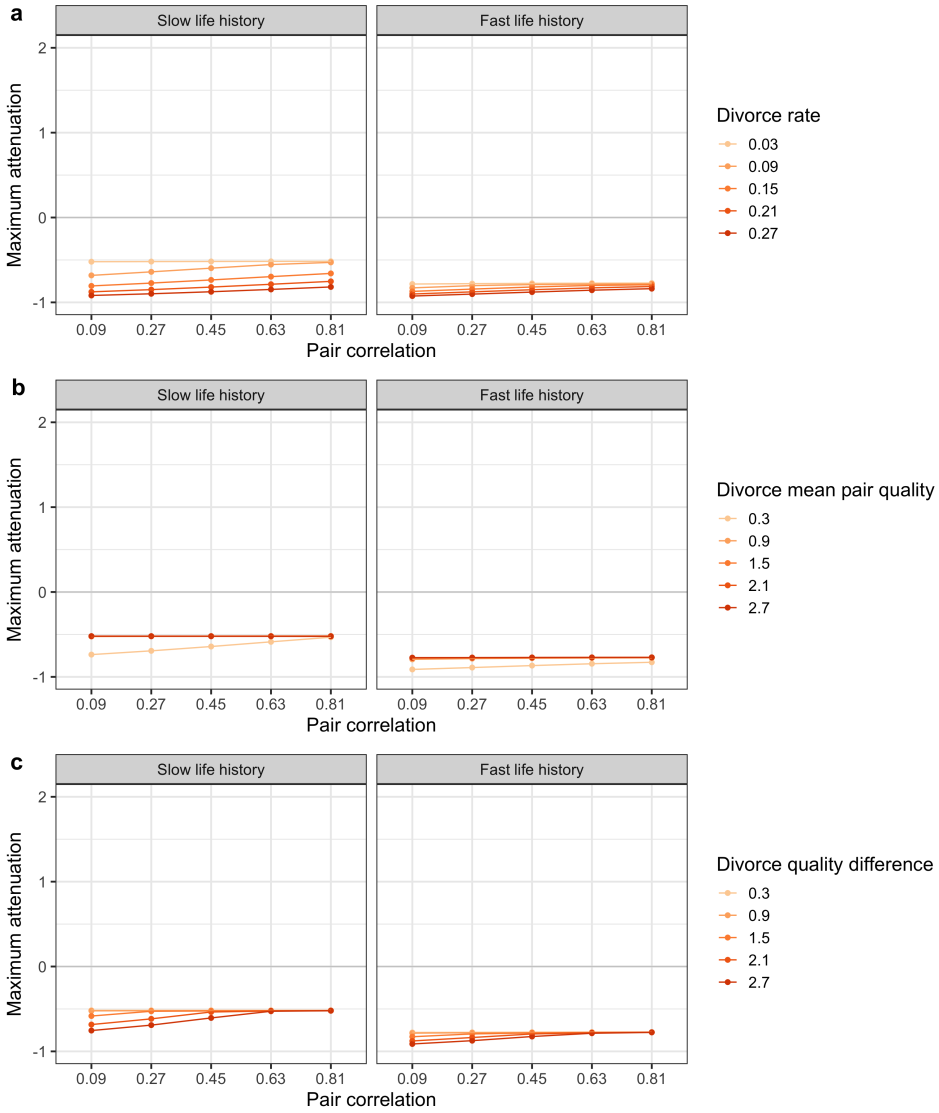

Figure S2.1: Maximum attenuation plotted against strength of pair correlation under slow and fast life histories, varying (a) baseline divorce rate, (b) influence of mean pair quality on divorce and (c) influence of pair quality difference on divorce.

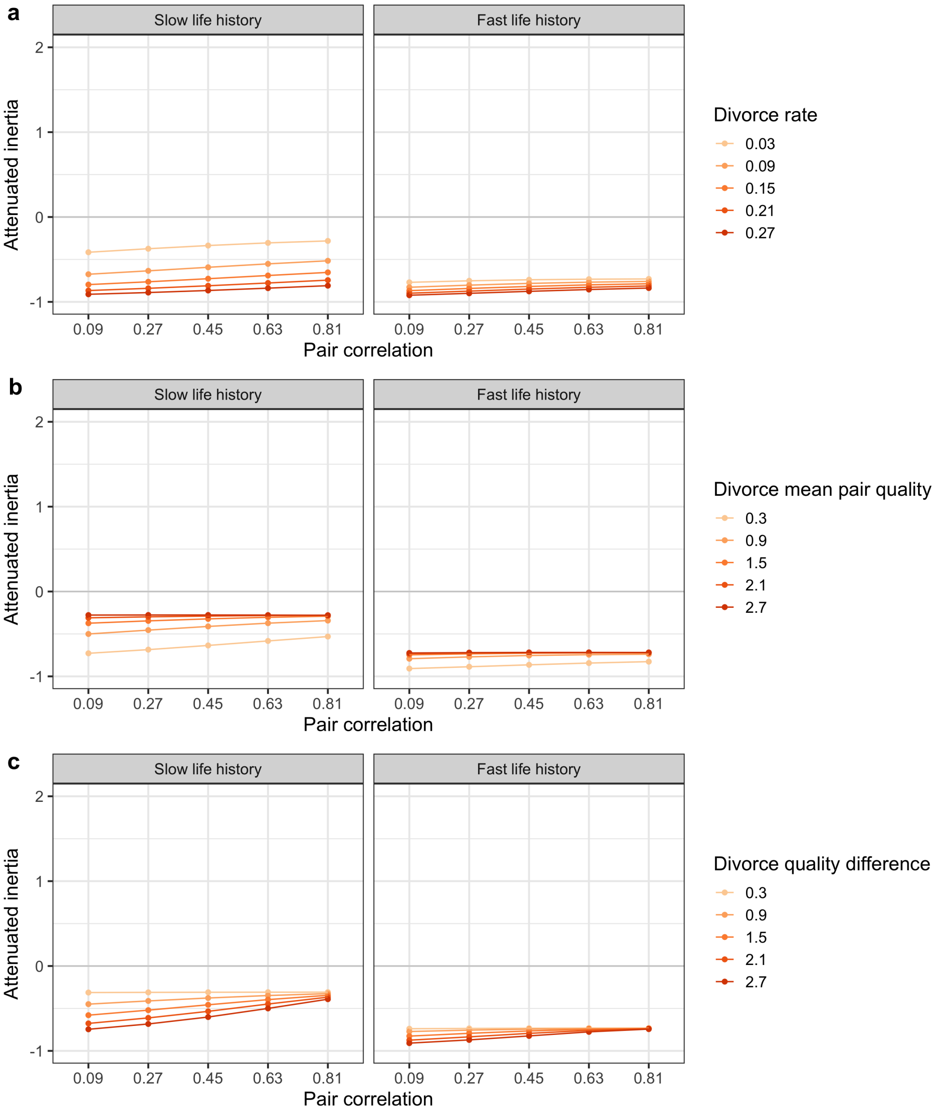

Figure S2.2: Attenuated inertia plotted against strength of pair correlation under slow and fast life histories, varying (a) baseline divorce rate, (b) influence of mean pair quality on divorce and (c) influence of pair quality difference on divorce.

Chapter 3

Bridging gaps in demographic analysis using phylogenetic imputation

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Abstract

Population responses to threats such as habitat loss, climate change and overexploitation are usually explored using demographic models parameterized with estimates of vital rates of survival, maturation and fecundity. However, the vital rate estimates required to construct such models are often unavailable, particularly for species of conservation concern. Phylogenetically informed imputation methods have rarely been applied to demographic data but may be a powerful tool for reconstructing vital rates for vertebrates. Here, we use standardized vital rate estimates for 50 bird species to assess the use of phylogenetic imputation to fill gaps in demographic data. We calculated imputation accuracy for vital rates excluded from the dataset either singly or in combination, with and without phylogeny, body mass and life history trait data. We used imputed vital rates to calculate demographic metrics, including generation time, to validate the use of imputation in demographic analyses. Covariance among vital rates and other trait data provided a strong basis to guide imputation of missing vital rates in birds, even in the absence of phylogenetic information. Accounting for phylogenetic relationships improved imputation accuracy for vital rates with high phylogenetic signal (Pagel's $\lambda > 0.8$). Importantly, including body mass and life history trait data compensated for lack of phylogenetic information. Estimates of demographic metrics were sensitive to the accuracy of imputed vital rates. Accurate demographic data and metrics such as generation time are needed to inform conservation planning processes, for example through IUCN Red List assessments and population viability analysis. Imputed vital rates could be useful in this context but, as for any estimated parameters, awareness of the

sensitivities of demographic model outputs to the imputed parameters is essential.

Keywords—conservation modelling, demographic models, parameter estimation, generation time, population growth rate, population dynamics, survival, extinction risk.

3.1 Introduction

Globally, biodiversity faces an unprecedented threat of extinction (Barnosky et al. 2011, Pimm et al. 2014, Ceballos et al. 2015), driven by human-induced threats such as habitat loss and degradation, climate change, and overexploitation (Brook et al. 2003, Parmesan 2006, Maclean and Wilson 2011, Maxwell et al. 2016). Understanding population responses to such threats is crucial for identifying at-risk species and to guide conservation interventions (e.g. Bruna et al. 2009, Dahlgren et al. 2016, Lunn et al. 2016). Population models parameterized with estimates of vital rates of survival, development and reproduction can be used to generate predictions about how a population will respond to pressures that cause changes to vital rates (Selwood et al. 2015).

Obtaining the vital rate estimates necessary to populate demographic models requires investment of resources and time, which may be lacking in a critical conservation setting. The most at-risk species may be those for which information is most lacking (Beissinger and Westphal 1998, Coulson et al. 2001, González-Suárez et al. 2012), due to geographical, taxonomic, or other biases in recording (Roberts et al. 2016, Troudet et al. 2017, dos Santos et al. 2020), or logistical barriers to collecting complete demographic data (Menges 2000, Weimerskirch 2002, Pike et al. 2008, Clutton-Brock and Sheldon 2010). Consequently, complete empirical demographic information represents only a small and biased subset of species (Lebreton et al. 2012, Salguero-Gómez et al. 2015, 2016, Conde et al. 2019).

When data are missing for a focal species, *ad hoc* methods are commonly used to fill in such gaps for demographic modelling (Beissinger and Westphal 1998). Parameter estimates may be derived from empirical data for other species based on relatedness (Heinsohn et al. 2004, Koenig 2008) or trait similarity (McCarthy et al. 1999, Valle et al. 2018). Other approaches include combining estimates from populations to form a representative model for a species (Sæther and Bakke 2000) or parameterization of models based on a range of plausible values (Rodríguez et al. 2004) or on data from captive individuals (e.g. Young et al. 2012).

Such approaches produce bias (Schafer and Graham 2002) and their use raises concerns about the reliability of model outputs and the ability to make robust conclusions (Sæther and Engen 2002, Ellner and Fieberg 2003, McGowan et al. 2011). Therefore, formal methods for estimating missing vital rates and quantifying uncertainty in such estimates are needed.

Many *ad hoc* methods of imputing missing values are based on the expectation that the vital rates of the focal species will be similar to closely related species (Felsenstein 1985, Pagel 1999). By accounting more formally for evolutionary history, we may be able to improve the imputation of missing vital rates. Phylogenetic imputation methods use phylogeny, together with an evolutionary model describing the divergence of trait values (Martins and Hansen 1997, Pagel 1999, Freckleton et al. 2002), to estimate missing values in species-based data. Traits may be more or less labile, leading to differences in how well trait values may be predicted by evolutionary relationships (Freckleton et al. 2002, Blomberg et al. 2003). Phylogenetic signal, a measure of the strength of phylogenetic dependence of trait values (Pagel 1999, Blomberg and Garland 2002), may determine the benefit of using phylogenetic information when imputing trait values (Penone et al. 2014). If phylogenetic signal is strong, phylogenetically informed methods can potentially improve imputation performance.

Phylogenetic imputation has been proposed for filling gaps in functional trait data in plants (Swenson 2014) and mammals (Guénard et al. 2013, Penone et al. 2014). Such methods have rarely been applied to demographic data, although hierarchical approaches incorporating taxonomy have been used to estimate life history parameters in fish (Thorson et al. 2017). Here, we focus on demographic traits, namely vital rates of survival, maturation, and fecundity. In plants, imputation of single vital rates suggested that neither fecundity nor the survival of different life stages were strongly predicted by phylogeny or species-level traits (Che-Castaldo et al. 2018), reflecting weak phylogenetic signal in plant vital rates (Burns et al. 2010). In vertebrates, strong phylogenetic signal in characteristics that covary with vital rates (body size, morphology and life history traits) has been interpreted as being informative about evolutionary processes such as the strength of stabilising selection and evolutionary lability (Blomberg et al. 2003; but see Revell et al. 2008). Whatever the exact evolutionary processes involved, the tendency of vital rates to covary with body size (Stearns 1983) and life history traits (e.g. age at maturity and clutch size, Sæther and Bakke 2000) suggests that they will also have strong phylogenetic signal, which would be useful in an applied setting to infer vital rates for related species. The inclusion of covarying allometric and life history trait data may help to inform the imputation of vital rates (e.g. Shine and Charnov 1992, Brawn et al. 1995).

Imputed vital rates provide a means by which demographic characteristics of a population may be derived. Demographic metrics of interest in a conservation setting include population growth rate and its sensitivity and elasticity to underlying vital rates (Benton and Grant 1999), and life history metrics such as generation time. Sensitivity analysis identifies vital rates with the most capacity to produce change in population growth rate. Accurate imputation of vital rates to which population growth rate is sensitive would be valuable for making well-founded demographic predictions to guide conservation interventions. Generation time is used by international conservation bodies such as the International Union for Conservation of Nature (IUCN) to produce indicators for conservation decision-making (Mace et al. 2008). When underlying life history data is missing or sparse, demographic metrics may be estimated using proxies based on life history parameters such as reproductive lifespan (Fung and Waples 2017, Staerk et al. 2019) or imputed either directly (Fagan et al. 2013, Cooke et al. 2018) or by means of underlying life history parameters (Pacifici et al. 2013, Bird et al. 2020). Demographic metrics derived using phylogenetically imputed vital rates could improve accuracy over these alternative methods.

Here, we use existing vital rate data for birds to assess the feasibility of using phylogenetic imputation to fill gaps in demographic analysis. While much avian demographic data has been compiled (Sæther and Bakke 2000, Lebreton et al. 2012, Salguero-Gómez et al. 2016), information about vital rates is missing for many species of conservation concern (e.g. survival is missing for 82% of bird species, Conde et al. 2019). We use complete demographic data for 50 species to derive standardized vital rates and apply a multivariate imputation framework which incorporates phylogenetic covariance among vital rates to impute missing values. We determine how accurately values excluded from the vital rate data can be imputed, either singly or in combination. Further, we assess the value of including body mass and life history trait data (clutch size and female age at maturity) when imputing missing vital rate data. We use original and imputed vital rates to calculate demographic metrics that inform assessments of population performance and extinction risk.

3.2 Methods

All analyses were carried out in R (version 3.6.3, R Core Team 2020).

3.2.1 Standardized vital rate, body mass and life history trait data

We extracted matrix population models for birds from COMADRE Animal Matrix Database (version 3.0.1, COMADRE) and other sources (Sæther and Bakke 2000). We screened the data to avoid models with errors in construction (Kendall et al. 2019) and to ensure valid structure for the subsequent analysis (Summary of supporting information). The resulting set of matrix population models represented 50 bird species across 15 orders and a range of avian life histories. We identified pre-breeding and post-breeding census models and categorized each life history as early maturation (individuals mature and breed after one year) or delayed maturation (individuals remain as non-breeding juveniles for one or more years) (Fujiwara and Diaz-Lopez 2017). Allowing for the different representation of early and delayed maturation species in pre-breeding and post-breeding census models, we collapsed pre-reproductive and reproductive stages (Salguero-Gómez and Plotkin 2010) and derived a set of standardized vital rates representing first year survival (s_0), adult survival (s_a), fecundity (f), and maturation rate (m) from the resulting matrices. To ensure a full set of standardized vital rates in the imputation analysis we restricted the main analysis to 40 species with post-breeding census models (Summary of supporting information). We combined the standardized vital rates with avian body mass, clutch size, and female age at maturity (Myhrvold et al. 2015, Wilman et al. 2014) and transformed all variables to satisfy the requirements of the imputation model (Summary of supporting information).

3.2.2 Phylogeny

We downloaded a sample of 1,000 full avian phylogenetic trees from the BirdTree website (www.birdtree.org, Jetz et al. 2012), pruned to match the species in the standardized vital rate data. The tree topology was well-supported (3 nodes with posterior probability < 0.95), so we used the least squares consensus method (Lapointe et al. 1997; phytools version 0.7-20, Revell 2012) to create an average tree for phylogenetic imputation analysis (Summary of supporting information). This method creates a consensus tree for which the sum-of-squares patristic (node-to-node) distances to the set of trees in the sample is minimized.

We compared outputs from imputation using the consensus tree with results for a sample of 50 trees from the posterior distribution to demonstrate that our results are insensitive to phylogenetic uncertainty (Summary of supporting information).

3.2.3 Phylogenetic signal

Phylogenetic signal is a measure of pattern derived by comparing observed trait distributions with expectations from a specified model of evolution. Pagel's λ is a transformation of the phylogeny, obtained by maximum likelihood, which produces the best fit of the data to a Brownian motion model of evolution. Pagel's λ takes values from 0 (complete phylogenetic independence) to 1 (patterns of similarity observed in the data are proportional to shared evolutionary history) or above (traits are more similar amongst species than expected) (Pagel 1999, Freckleton et al. 2002). We used phytools (version 0.7-20, Revell 2012) to estimate mean Pagel's λ for each standardized vital rate across 1000 phylogenetic trees obtained from BirdTree to account for any residual uncertainty in branch lengths. In addition, we used Rphylopars (version 0.2.12, Goolsby et al. 2016) to estimate Pagel's λ for each of the trait datasets to characterize phylogenetic dependence in the data, taking into account covariance among the data.

3.2.4 Phylogenetic imputation

We carried out a multi-stage analysis to assess the use of phylogenetic imputation to reconstruct missing values introduced systematically into the standardized vital rate data (Fig. 3.1). Phylogenetic imputation predicts missing values based on covariance among the data, supplemented by phylogeny and a model for evolution. We used Rphylopars (version 0.2.12, Goolsby et al. 2016), which implements maximum likelihood estimation of missing trait values in a phylogenetic generalized least squares framework, assuming normally distributed continuous variables. We combined the consensus phylogeny with a null model of evolution, in which phylogeny does not influence trait values, and a Pagel's λ model, which incorporates phylogenetic dependence (Phylogeny, Fig. 3.1). We created three trait datasets: standardized vital rates only; vital rates and body mass data; and vital rates, body mass and life history trait data (Trait datasets, Fig. 3.1). Within each trait dataset, we introduced a known structure of missing values among the vital rates for a focal species. We removed

Figure 3.1: We applied phylogenetic imputation to vital rate, body mass and life history trait data to assess the accuracy of predicting vital rates for use in demographic models. Our key questions related to phylogeny, trait data, and missing data structure. 1. Does including phylogenetic relationships among species improve predictions of vital rates? We used a consensus phylogenetic tree and imputed vital rates under two alternative evolutionary models: a null model which assumes that phylogenetic relationships have no influence on trait values, and Pagel's λ, in which the phylogeny is scaled to account for phylogenetic dependence in the data. 2. What is the value of including additional body mass and life history trait data when imputing missing vital rates? We used three alternative trait datasets for imputation: a baseline dataset containing standardized vital rate data and two extended datasets which added body mass and life history trait data, retaining complete cases only. 3. How are predictions affected by how many, and which, vital rates are missing? For each focal species, we removed vital rate data systematically in combinations of single and multiple missing vital rates and used phylogenetic imputation to reconstruct the missing values. 4. We calculated imputation accuracy for each focal vital rate, missing vital rate combination, trait dataset and evolutionary model.

Population growth metrics	
Asymptotic population growth rate	Long-term performance of a population
Sensitivity and elasticity of population growth rate	Response of population growth rate to changes in underlying vital rates

Life history metrics	
Generation time	Time required for the population to increase by a factor equal to the net reproductive rate
Mean age at maturity	Average time taken to enter the reproductive stage
Mean lifespan	Average age of individuals at death

Table 3.1: We used imputed vital rates to parameterise matrix population models and calculated demographic metrics of population growth and life history (Caswell 2001) to assess the effect of imputed parameters on demographic model outputs.

vital rate values in all possible combinations of single and multiple vital rates, resulting in 15 datasets per species (Missing data combinations, Fig. 3.1). We imputed missing values assuming either model of evolution. After transformation to the original scale for each vital rate, we used the normalized root mean square error (NRMSE),

$$\text{NRMSE} = \frac{\sqrt{\frac{\sum_i (X_i^* - X_i)^2}{n}}}{\max_i(X_i) - \min_i(X_i)}, \tag{3.1}$$

to assess imputation accuracy for each vital rate, missing vital rate combination and trait dataset. Here, X_i^* and X_i represent the imputed and original values, respectively, of a vital rate for species i. Normalisation by the range of observed values for the vital rate allows comparison of errors across vital rates.

We used species means to estimate phylogenetic covariance (Goolsby et al. 2016) to avoid conditioning problems in the datasets which included body mass and life history trait data. We imputed values both with and without phenotypic variation for the vital rate data to demonstrate that excluding phenotypic covariance from the analysis was not detrimental to the estimation of phylogenetic covariance (Summary of supporting information).

3.2.5 Demographic metrics

We represented avian life histories using stage-structured, post-breeding census models with an annual time step (Caswell 2001) parameterized with first year survival (s_0), adult survival (s_a), fecundity (f), and maturation rate (m) imputed under the phylogenetic model. For early maturation species,

$$\mathbf{A} = \begin{bmatrix} s_0 f & s_a f \\ s_0 & s_a \end{bmatrix}, \tag{3.2}$$

and for delayed maturation species,

$$\mathbf{A} = \begin{bmatrix} 0 & m\, s_a f & s_a f \\ s_0 & (1-m)\, s_a & 0 \\ 0 & m\, s_a & s_a \end{bmatrix}. \tag{3.3}$$

We used these population models to generate population growth and life history metrics (Table 3.1). For each missing data combination and trait dataset, we calculated the normalized root mean square error (Equation 3.1) to compare estimates of these demographic metrics from models parameterized with imputed and original vital rates. We inspected differences in the sensitivity and elasticity of population growth rate to each vital rate for bias (systematic differences) or increased variance.

3.3 Results

3.3.1 Phylogenetic signal

For post-breeding census data, mean Pagel's λ was weak for first year survival (0.246, SD 0.013), intermediate for fecundity (0.532, SD 0.018), and strong for adult survival (0.889, SD 0.016) and maturation rate (0.923, SD 0.116). Mean values for pre-breeding census data were similar (s_a: 0.817, SD 0.019; m: 0.934, SD 0.094). High phylogenetic signal suggests that adult survival and maturation rate should be successful targets for phylogenetic imputation but high variance in Pagel's λ for maturation rate suggested greater phylogenetic uncertainty in maturation rate.

For post-breeding census models, Pagel's λ was 0.488 for the vital rate data, increasing to 0.702 when body mass was added, and decreasing to 0.684 when life history trait data was

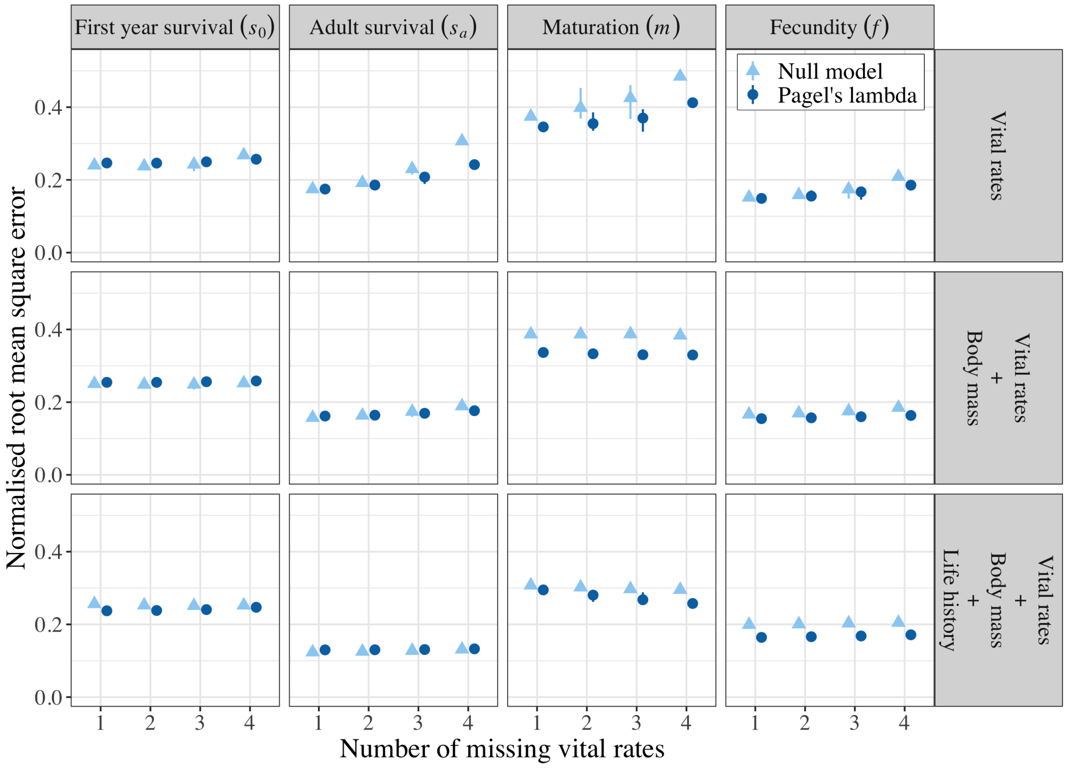

Figure 3.2: Adult survival and fecundity were the most accurately imputed vital rates under different missing vital rates, trait dataset, and evolutionary model. When multiple vital rates were missing, phylogenetic information or body mass and life history trait data improved accuracy of imputed adult survival and maturation rates. Points show the mean errors across combinations of the same number of missing vital rates and error bars indicate the range of normalized root mean square error for different missing vital rate combinations.

included, with a similar pattern for pre-breeding census data. These results indicate that body mass improves the characterization of phylogenetic dependence among vital rates, but life history trait data does not produce any further improvement and may even act slightly negatively on phylogenetic signal.

3.3.2 Imputed vital rates

Adult survival and fecundity were the most accurately imputed vital rates in the post-breeding census data, with mean NRMSE of 0.169 (SD 0.039) and 0.172 (SD 0.019) respectively). Imputed first year survival (mean NRMSE: 0.248, SD 0.010) and maturation rate (mean NRMSE: 0.346, SD 0.055) had poorer accuracy.

For first year survival and fecundity, the phylogenetic model was no more accurate than the null model (Fig. 3.2). However, phylogenetic information helped to improve imputation

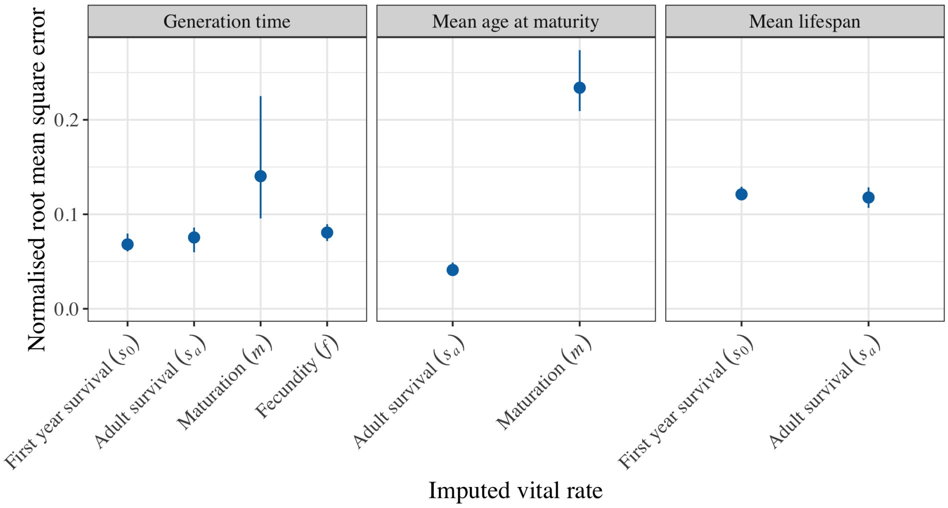

Figure 3.3: Life history metrics calculated from matrix population models parameterized with imputed vital rates varied in accuracy according to the contribution of the imputed vital rate to the life history metric. Imputed vital rates which did not have an effect on the life history metric estimate are not shown. Points show the mean errors across trait datasets and error bars indicate the range of normalised root mean square error for different trait datasets.

accuracy for adult survival and maturation rate, particularly for multiple missing vital rates.

Including body mass and life history trait data improved imputation accuracy for adult survival and maturation rate (Fig. 3.2) and reduced the difference in accuracy between phylogenetic and null models for adult survival.

3.3.3 Life history metrics

Generation time

Generation time calculated with a single imputed vital rate had a similar accuracy across trait datasets for first year survival, adult survival and fecundity (mean NRMSE: 0.075, SD 0.011, Fig. 3.3), despite differences in imputation accuracy for these vital rates (Fig. 3.2). For maturation rate, mean NRMSE was higher (0.140, SD 0.073) and NRMSE was markedly higher when body mass and life history trait data were included, due to two outliers for which imputed maturation rate was under-estimated, leading to over-estimation of generation time (Summary of supporting information).

Mean age at maturity

Mean age at maturity was sensitive to imputed adult survival because we assumed juvenile survival to be equal to adult survival, but it was relatively well characterized when adult survival was imputed (mean NRMSE: 0.041, SD 0.007, Fig. 3.3). For imputed maturation rate, mean age at maturity was not well estimated (mean NRMSE: 0.234, SD 0.035) and, as for generation time, mean age at maturity was less accurate when life history data was included due to two outliers for which the metric was over-estimated (Summary of supporting information).

Mean lifespan

Mean lifespan had similar accuracy when either first year or adult survival were unknown (mean NRMSE: 0.121, SD 0.007, and 0.118, SD 0.011, respectively) and was not influenced by adding body mass and life history trait data.

3.3.4 Population growth metrics

Population growth rate

When maturation rate was imputed, population growth rate matched the original values reasonably well (mean NRMSE: 0.051, SD $<$ 0.001 Fig. 3.4). Population growth rate was less accurate when first year or adult survival were imputed (mean NRMSE: 0.125, SD 0.010, and 0.126, SD 0.014, respectively). The least accurate results arose when fecundity was imputed (mean NRMSE: 0.221, SD 0.039) driven by over-estimation of fecundity for a single species (Summary of supporting information).

Sensitivity and elasticity of population growth rate

Estimates of the sensitivity of population growth rate to the underlying vital rates varied in accuracy across missing vital rates and focal vital rate for the sensitivity calculation (Fig. 3.4). Responses to imputed vital rates were more consistent across vital rate elasticities, with greatest accuracy for maturation rate (mean NRMSE: 0.042, SD 0.009) and adult survival (mean NRMSE: 0.060, SD 0.019) and least accuracy for first year survival (mean NRMSE: 0.105, SD 0.013) and fecundity (mean NRMSE: 0.161, SD 0.027). Errors in sensitivities and elas-

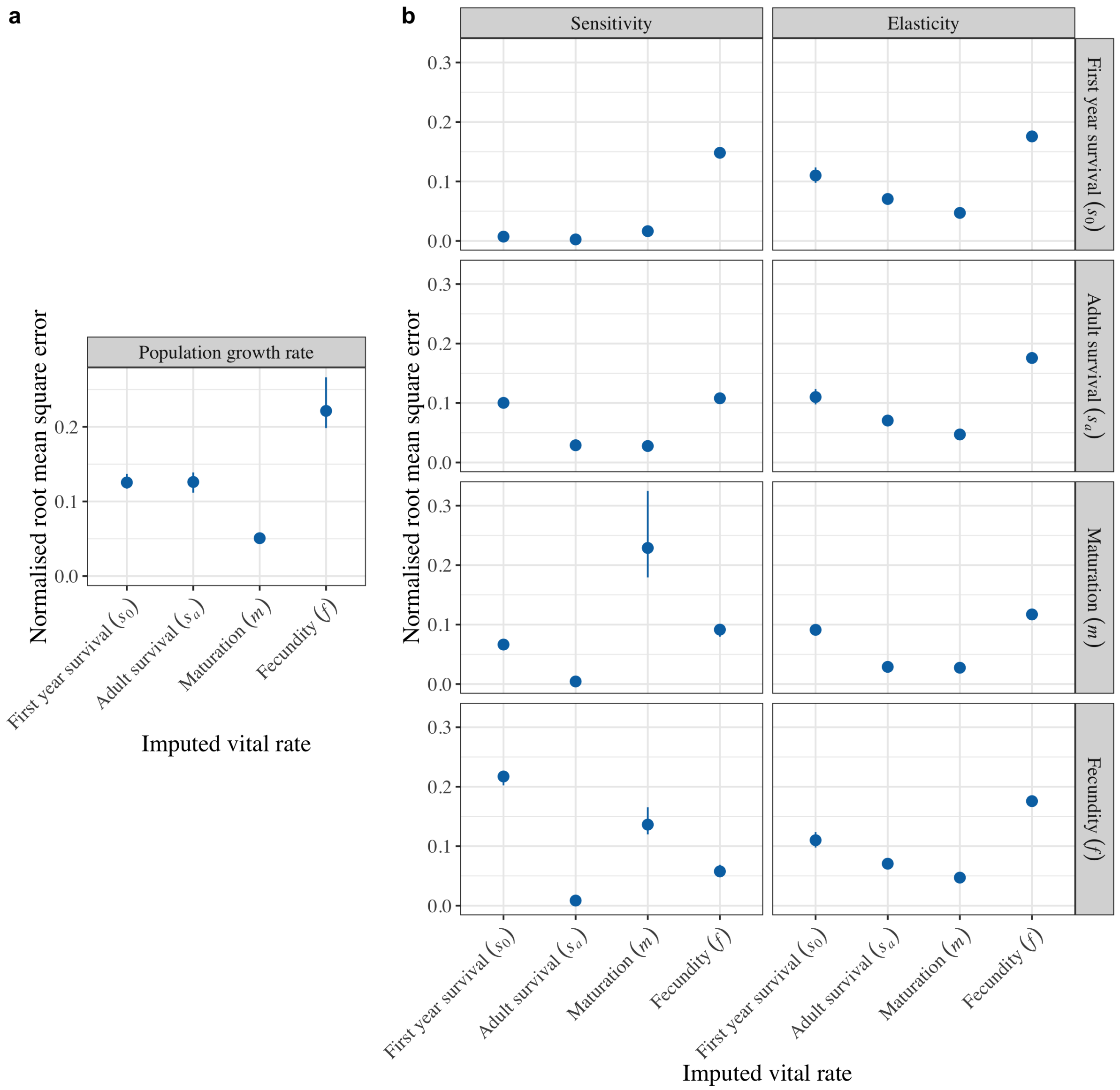

Figure 3.4: Estimates of population growth rate (a) and sensitivity and elasticity of population growth rate to underlying vital rates (b) varied in accuracy when vital rates were imputed, with imputed fecundity causing the least accurate values in many cases. Accuracy was similar across trait datasets except in two cases when life history trait data reduced the accuracy of the demographic metric. Points show the mean errors across trait dataset and error bars indicate the range of normalised root mean square error for different trait datasets.

ticities were unbiased except when maturation rate was imputed (Summary of supporting information).

3.4 Discussion

Detailed understanding of species' responses to global change, which is needed to address the current biodiversity crisis, is limited by gaps in the demographic data needed to predict population trajectories (Kindsvater et al. 2018, Conde et al. 2019). Efforts such as the IUCN Red List (IUCN 2020) are designed to make the most of limited information (Rodrigues et al. 2006, Mace et al. 2008) but the use of proxies to compensate for missing data can result in bias and under- or over-estimation of threat level (Fung and Waples 2017, Staerk et al. 2019). Accurate estimation of vital rates, particularly those to which elasticity of population growth rate is high, such as adult survival in long-lived species, is important for reliable predictions of population performance. We evaluated the use of phylogenetic imputation to replace missing vital rate data in birds. We found that applying a multivariate framework which accounted for covariance among rates of survival, reproduction, and maturation allowed us to impute some missing vital rates relatively well, even in the absence of phylogenetic information. Including phylogenetic relationships improved the accuracy of imputed values in some cases. However, auxiliary trait data also tended to improve imputation accuracy for multiple vital rates and compensated for lack of phylogeny in most cases.

Imputation accuracy did not reflect the ranking of vital rates by phylogenetic signal. However, vital rates with the strongest phylogenetic signal, adult survival and maturation rate, improved in accuracy with phylogeny, particularly for multiple missing vital rates. Penone et al. (2014) linked the influence of phylogeny on trait estimates in carnivores both to phylogenetic signal and to how much traits covaried with body size. We found that imputation accuracy deteriorated for multiple missing vital rates, suggesting that covariance patterns among the vital rates were important.

Imputation tended to over-estimate maturation rates (Summary of supporting information). In discrete time, stage-based population models, species that mature in a single time step have a maturation rate of 1, while for species with delayed onset of reproduction, maturation rate can be markedly less than 1. The resulting bimodal distribution is severely non-normal, even after transformation. The imputation model used here estimates covariance among normally distributed variables and was unable to compensate for this unusual distribution.

Our finding that body mass and life history trait data improved the accuracy of imputed values contrasts with studies which demonstrate relatively minor effects of species-level traits on the estimation of demographic rates. For example, body mass did not improve estimation of *per capita* population growth rate in mammals (Fagan et al. 2013) and in plants, size and growth form largely failed to improve predictability of demographic rates (Che-Castaldo et al. 2018).

We found that accuracy of demographic metrics typically used for conservation assessment purposes, such as generation time (Mace et al. 2008), depended both on the accuracy of imputed values and on the sensitivity of the metric to the imputed vital rates. Moreover, the simplified life cycle underlying our approach may introduce bias in some demographic outputs (Fujiwara and Diaz-Lopez 2017). Many studies have advised caution in the interpretation of demographic model outputs due to parameter uncertainty (Beissinger and Westphal 1998, Ellner et al. 2002, Reed et al. 2002); similar care is necessary for models parameterized with imputed values.

Our results are limited by the availability and partiality of demographic data (Salguero-Gómez et al. 2015, 2016, Conde et al. 2019), which inform estimates of covariance among vital rates. Including data for more species might improve accuracy of imputed vital rates by strengthening patterns of covariance (e.g. Penone et al. 2014). However, vital rate data may be missing not at random (MNAR) for species of conservation concern, and such biases in missing values can influence comparative analyses by skewing trait distributions (Nakagawa and Freckleton 2008, González-Suárez et al. 2012). Although geographical variation in demographic traits (e.g. differences in clutch size and survival across latitudes) could create different patterns of covariance among vital rates, including phylogeny, life history traits, and latitude may be sufficient to control for such variation (Jetz et al. 2008, Scholer et al. 2020). Future studies could use a broader coverage of avian life history to investigate how biases in the availability of demographic data affect imputation accuracy and could assess imputation of vital rates in other taxonomic groups.

Recommendations

The success of phylogenetic imputation rests on the validity of the data covariance structure. This structure is determined by the phylogeny, and by the known values for vital rates and important covariates like body size. Thus, the quantity and accuracy of these data may strongly influence the reliability of imputed values. We suggest exploring the impact of uncertainty in the input data by, for example, varying the values within reasonable limits to determine the sensitivity of outputs. Uncertainty in the phylogeny could be explored in a similar way by sampling from a distribution of plausible trees.

We found that maturation rate was poorly handled by the distributional assumptions of the imputation method. We advise the use of an alternative approach such as using a two-component mixture model to capture the bimodal distribution for maturation rate.

We have provided a qualitative assessment of how differences in the accuracy of imputed vital rates translate to accuracy of demographic metrics. A global sensitivity analysis could be used to quantify how uncertainty propagates from imputed vital rates to demographic metrics.

We have demonstrated a novel approach to bridging gaps in demographic analysis using phylogenetic imputation. While this method cannot replace demographic metric calculation when detailed age-specific life history parameters are available, the ability to impute vital rates for species with sparse demographic data is valuable in a data-limited conservation context and avoids biases associated with assuming family or genus based mean values for underlying traits (Schafer and Graham 2002). Accurate demographic information is vital for indicators such as the IUCN Red List, which informs conservation decision-making from species-level conservation to spatial prioritization (Rodrigues et al. 2006), and the IUCN Green List, a framework for assessing species recovery and conservation success (Akçakaya et al. 2018). In addition, data-driven assessments are essential in guiding business processes and supporting sustainable development goals (Brooks et al. 2015, Bennun et al. 2018).

3.5 Summary of supporting information

Data extraction procedure, species list, phylogenetic tree, and taxonomic bias (Appendices S3.1–S3.4); exploration of phylogenetic uncertainty (Appendix S3.5); comparison of imputation with and without phenotypic variation (Appendix S3.6); observed vs imputed vital rates for post-breeding census data under the null (Appendices S3.7–S3.10) and phylogenetic (Appendices S3.11–S3.14) models; observed vs imputed vital rates for pre-breeding census data under the null and phylogenetic models (Appendices S3.15–S3.16); and results for life history (Appendices S3.17–S3.19) and population growth (Appendices S3.20–S3.22) metrics are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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3.7 Author contributions

T.D.J., R.S.G., O.R.J., D.Z.C. and A.P.B. designed the study. T.D.J. prepared the data, carried out the analysis and wrote the manuscript. All co-authors provided critical feedback and approved the manuscript for publication.

3.8 References

Akçakaya HR, et al. 2018. Quantifying species recovery and conservation success to develop an IUCN Green List of Species. *Conservation Biology*, **32**(5), 1128–1138.

Barnosky AD, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature*, **471**(7336), 51–57.

Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability in endangered species management. *The Journal of Wildlife Management*, **62**(3), 821–841.

Bennun L, et al. 2018. The value of the IUCN Red List for business decision-making. *Conservation Letters*, **11**(1), e12353.

Benton TG, Grant A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution*, **14**(12), 467–471.

Bird JP, Martin R, Akçakaya HR, Gilroy J, Burfield IJ, Garnett ST, Symes A, Taylor J, Şekercioğlu ÇH, Butchart SHM. 2020. Generation lengths of the world's birds and their implications for extinction risk. *Conservation Biology*, **34**(5), 1252–1261.

Blomberg EJ, Tefft BC, Reed JM, McWilliams SR. 2012. Evaluating spatially explicit viability of a declining ruffed grouse population. *The Journal of Wildlife Management*, **76**(3), 503–513.

Blomberg SP, Garland T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, **15**(6), 899–910.

Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**(4), 717–745.

Brawn JD, Karr JR, Nichols JD. 1995. Demography of birds in a neotropical forest: effects of allometry, taxonomy, and ecology. *Ecology*, **76**(1), 41–51.

Brook BW, Sodhi NS, Ng PKL. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**(6947), 420–423.

Brooks TM, Butchart SHM, Cox NA, Heath M, Hilton-Taylor C, Hoffmann M, Kingston N, Rodríguez JP, Stuart SN, Smart J. 2015. Harnessing biodiversity and conservation knowledge products to track the Aichi Targets and Sustainable Development Goals. *Biodiversity*, **16**(2-3), 157–174.

Bruna EM, Fiske IJ, Trager MD. 2009. Habitat fragmentation and plant populations: is what we know demographically irrelevant? *Journal of Vegetation Science*, **20**(3), 569–576.

Burns JH, Blomberg SP, Crone EE, Ehrlén J, Knight TM, Pichancourt JB, Ramula S, Wardle GM, Buckley YM. 2010. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *Journal of Ecology*, **98**(2), 334–344.

Caswell H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Mass., 2nd ed.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances*, **1**(5), e1400253.

Chamberlain SA, Szöcs E. 2013. taxize: taxonomic search and retrieval in R. *F1000Research*. doi: 10.12688/f1000research.2-191.v2.

Che-Castaldo J, Che-Castaldo C, Neel MC. 2018. Predictability of demographic rates based on phylogeny and biological similarity. *Conservation Biology*, **32**(6), 1290–1300.

Clutton-Brock T, Sheldon BC. 2010. The seven ages of Pan. *Science*, **327**(5970), 1207–1208.

COMADRE. 2019. COMADRE Animal Matrix Database (v.3.0.1). Available from: https://www.compadre-db.org (accessed on 19 April 2020).

Conde DA, et al. 2019. Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences*, **116**(19), 9658–9664.

Cooke RSC, Gilbert TC, Riordan P, Mallon D. 2018. Improving generation length estimates for the IUCN Red List. *PLOS ONE*, **13**(1), e0191770.

Coulson T, Mace GM, Hudson E, Possingham H. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution*, **16**(5), 219–221.

Dahlgren DK, Guttery MR, Messmer TA, Caudill D, Dwayne Elmore R, Chi R, Koons DN. 2016. Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation. *Ecosphere*, **7**(3), e01249.

dos Santos JW, Correia RA, Malhado ACM, Campos-Silva JV, Teles D, Jepson P, Ladle RJ. 2020. Drivers of taxonomic bias in conservation research: a global analysis of terrestrial mammals. *Animal Conservation*.

Ellner SP, Fieberg J. 2003. Using PVA for management despite uncertainty: effects of habitat, hatcheries, and harvest on salmon. *Ecology*, **84**(6), 1359–1369.

Ellner SP, Fieberg J, Ludwig D, Wilcox C. 2002. Precision of population viability analysis. *Conservation Biology*, **16**(1), 258–261.

Fagan WF, Pearson YE, Larsen EA, Lynch HJ, Turner JB, Staver H, Noble AE, Bewick S, Goldberg EE. 2013. Phylogenetic prediction of the maximum per capita rate of population growth. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**(1763), 20130523.

Felsenstein J. 1985. Phylogenies and the comparative method. *The American Naturalist*, **125**(1), 1–15.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**(6), 712–726.

Fujiwara M, Diaz-Lopez J. 2017. Constructing stage-structured matrix population models from life tables: comparison of methods. *PeerJ*, **5**, e3971.

Fung HC, Waples RS. 2017. Performance of IUCN proxies for generation length. *Conservation Biology*, **31**(4), 883–893.

González-Suárez M, Lucas PM, Revilla E. 2012. Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology*, **81**(6), 1211–1222.

Goolsby EW, Bruggeman J, Ane C. 2016. Rphylopars: phylogenetic comparative tools for missing data and within-species variation. R package version 0.2.12. Available from CRAN.R-project.org/package=Rphylopars (accessed May 2020).

Guénard G, Legendre P, Peres-Neto P. 2013. Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution*, **4**(12), 1120–1131.

Heinsohn R, Lacy RC, Lindenmayer DB, Marsh H, Kwan D, Lawler IR. 2004. Unsustainable harvest of dugongs in Torres Strait and Cape York (Australia) waters: two case studies using population viability analysis. *Animal Conservation forum*, **7**(4), 417–425.

Holmes DJ, Thomson SL, Wu J, Ottinger MA. 2003. Reproductive aging in female birds. *Experimental Gerontology*, **38**(7), 751–756.

IUCN. 2020. The IUCN Red List of Threatened Species. Tech. Rep. Version 2020-1, International Union for Conservation of Nature, Gland, Switzerland. Available from https://www.iucnredlist.org (accessed May 2020).

Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch size across species and space. *PLOS Biology*, **6**(12), e303.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature*, **491**(7424), 444–448.

Jones OR, et al. 2014. Diversity of ageing across the tree of life. *Nature*, **505**(7482), 169–173.

Kendall BE, Fujiwara M, Diaz-Lopez J, Schneider S, Voigt J, Wiesner S. 2019. Persistent problems in the construction of matrix population models. *Ecological Modelling*, **406**, 33–43.

Kindsvater HK, Dulvy NK, Horswill C, Juan-Jordá MJ, Mangel M, Matthiopoulos J. 2018. Overcoming the data crisis in biodiversity conservation. *Trends in Ecology & Evolution*, **33**(9), 676–688.

Koenig SE. 2008. Black-billed Parrot (*Amazona agilis*) population viability assessment (PVA): a science-based prediction for policy makers. *Ornitología Neotropical*, **19**, 135–149.

Lapointe FJ, Cucumel G, Baum D. 1997. The average consensus procedure: combination of weighted trees containing identical or overlapping sets of taxa. *Systematic Biology*, **46**(2), 306–312.

Lebreton JD, Devillard S, Popy S, Desprez M, Besnard A, Gaillard JM. 2012. Towards a vertebrate demographic data bank. *Journal of Ornithology*, **152**(2), 617–624.

Lunn NJ, Servanty S, Regehr EV, Converse SJ, Richardson E, Stirling I. 2016. Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. *Ecological Applications*, **26**(5), 1302–1320.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland E, Stuart SN. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**(6), 1424–1442.

Maclean IMD, Wilson RJ. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences*, **108**(30), 12337–12342.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, **149**(4), 646–667.

Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, **536**(7615), 143–145.

McCarthy MA, Webster A, Loyn RH, Lowe KW. 1999. Uncertainty in assessing the viability of the Powerful Owl *Ninox strenua* in Victoria, Australia. *Pacific Conservation Biology*, **5**(2), 144–154.

McGowan CP, Runge MC, Larson MA. 2011. Incorporating parametric uncertainty into population viability analysis models. *Biological Conservation*, **144**(5), 1400–1408.

Menges ES. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology & Evolution*, **15**(2), 51–56.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, **96**(11), 3109–3109.

Nakagawa S, Freckleton RP. 2008. Missing inaction: the dangers of ignoring missing data. *Trends in Ecology & Evolution*, **23**(11), 592–596.

Pacifici M, Santini L, Marco MD, Baisero D, Francucci L, Marasini GG, Visconti P, Rondinini C. 2013. Generation length for mammals. *Nature Conservation*, **5**, 89–94.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature*, **401**(6756), 877–884.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**(1), 637–669.

Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC. 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution*, **5**(9), 961–970.

Pike DA, Pizzatto L, Pike BA, Shine R. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology*, **89**(3), 607–611.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**(6187), 1246752.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reed JM, Mills LS, Dunning Jr JB, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett MC, Miller P. 2002. Emerging issues in population viability analysis. *Conservation Biology*, **16**(1), 7–19.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**(2), 217–223.

Revell LJ, Harmon LJ, Collar DC. 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, **57**(4), 591–601.

Ricklefs RE. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *The Condor*, **102**(1), 9–22.

Roberts BEI, Harris WE, Hilton GM, Marsden SJ. 2016. Taxonomic and geographic bias in conservation biology research: a systematic review of wildfowl demography studies. *PLOS ONE*, **11**(5), e0153908.

Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M, Brooks TM. 2006. The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution*, **21**(2), 71–76.

Rodríguez J, Fajardo L, Herrera I, Sánchez A, Reyes A. 2004. Yellow-shouldered Parrot (*Amazona barbadensis*) on the islands of Margarita and La Blanquilla, Venezuela. In Akçakaya HR, Burgman MA, Kindvall O, Wood CC, Sjogren-Gulve P, Hatfield JS, McCarthy MA, eds., *Species conservation and management: case studies*, pp. 361–370. Oxford University Press, Oxford.

Sæther BE, Bakke Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**(3), 642–653.

Sæther BE, Engen S. 2002. Pattern of variation in avian population growth rates. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **357**(1425), 1185–1195.

Salguero-Gómez R, et al. 2016. COMADRE: a global data base of animal demography. *Journal of Animal Ecology*, **85**(2), 371–384.

Salguero-Gómez R, et al. 2015. The COMPADRE Plant Matrix Database: an open online repository for plant demography. *Journal of Ecology*, **103**(1), 202–218.

Salguero-Gómez R, Plotkin JB. 2010. Matrix dimensions bias demographic inferences: implications for comparative plant demography. *The American Naturalist*, **176**(6), 710–722.

Schafer JL, Graham JW. 2002. Missing data: our view of the state of the art. *Psychological Methods*, **7**(2), 147–177.

Scholer MN, Strimas-Mackey M, Jankowski JE. 2020. A meta-analysis of global avian survival across species and latitude. *Ecology Letters*, **23**(10), 1537–1549.

Selwood KE, McGeoch MA, Mac Nally R. 2015. The effects of climate change and land-use change on demographic rates and population viability. *Biological Reviews*, **90**(3), 837–853.

Shine R, Charnov EL. 1992. Patterns of survival, growth, and maturation in snakes and lizards. *The American Naturalist*, **139**(6), 1257–1269.

Staerk J, Conde DA, Ronget V, Lemaitre JF, Gaillard JM, Colchero F. 2019. Performance of generation time approximations for extinction risk assessments. *Journal of Applied Ecology*, **56**(6), 1436–1446.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**(2), 173–187.

Swenson NG. 2014. Phylogenetic imputation of plant functional trait databases. *Ecography*, **37**(2), 105–110.

Thorson JT, Munch SB, Cope JM, Gao J. 2017. Predicting life history parameters for all fishes worldwide. *Ecological Applications*, **27**(8), 2262–2276.

Tirpak JM, et al. 2006. Ruffed grouse population dynamics in the central and southern Appalachians. *Biological Conservation*, **133**(3), 364–378.

Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F. 2017. Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, **7**(1), 9132.

Valle S, Collar NJ, Harris WE, Marsden SJ. 2018. Trapping method and quota observance are pivotal to population stability in a harvested parrot. *Biological Conservation*, **217**, 428–436.

Weimerskirch H. 2002. Seabird demography and its relationship with the marine environment. In Schreiber EA, Burger J, eds., *Biology of Marine Birds*, pp. 115–135. CRC Press.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, **95**(7), 2027–2027.

Young AM, Hobson EA, Lackey LB, Wright TF. 2012. Survival on the ark: life-history trends in captive parrots. *Animal Conservation*, **15**(1), 28–43.

Yu G, Lam TTY, Zhu H, Guan Y. 2018. Two methods for mapping and visualizing associated data on phylogeny using ggtree. *Molecular Biology and Evolution*, **35**(2), 3041–3043.

Yu G, Smith DK, Zhu H, Guan Y, Lam TTY. 2017. ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution*, **8**(1), 28–36.

3.9 Supporting information

Appendix S3.1 Data extraction

We extracted demographic data for 15 bird species from the COMADRE Animal Matrix Database (version 3.0.1, COMADRE). We selected records for which the matrix population models conformed to the following requirements to ensure valid structure for the subsequent analysis. We required that the survival component of the matrix did not contain any column sums greater than 1, since the proportion of individuals surviving in each stage class cannot exceed 1; all transition probabilities and *per-capita* sexual reproductive events were represented; transitions for survival/development and fertility were represented separately; the model represented a single sex; and the model did not include migration. We considered only matrices representing wild populations which were not subject to any treatments, so that the vital rates would be representative of natural population dynamics. In addition, we removed matrix population models which included vital rate estimates from multiple species or populations, a common way of filling gaps in demographic data (e.g. Blomberg et al. 2012). We examined the models that met these requirements and excluded any matrices which contained errors in construction (Kendall et al. 2019). We derived matrix population models for an additional 35 species from demographic data provided by Sæther and Bakke (2000), excluding records which were already included in the COMADRE data or which combined vital rate estimates for different populations. The resulting set of matrix population models covered 50 unique bird species across 15 orders (Table S3.2, Fig. S3.3). The selection showed some taxonomic bias, notably under-representation in Passeriformes, and over-representation in Charadriiformes, Acciptriformes, Anseriformes and some other orders (Fig. S3.4), suggesting a tendency for population studies to focus on larger and longer-lived bird species.

To allow comparison of vital rates across species we proposed a simple life cycle with vital rates aggregated into pre-reproductive and reproductive stages. Although reproductive senescence is known in birds (Holmes et al. 2003, Jones et al. 2014), none of the models in the analysis included post-reproductive stages. Allowing for the different representation of early and delayed maturation species in pre-breeding and post-breeding census models, we collapsed pre-reproductive and reproductive stages (Salguero-Gómez and Plotkin 2010) and derived a set of standardized vital rates representing first year survival (s_0), adult survival (s_a), fecundity (f), and maturation rate (m) from the resulting matrices. We found that aggregate juvenile survival for delayed maturation species was collinear with adult survival so we did not include this survival rate in the set of standardized vital rates. For pre-breeding census matrix models, fertility terms are a product of per-capita fecundity and first year survival, so these standardized vital rates could not be extracted separately. Hence, we restricted the main analysis to 40 species with post-breeding census models (Table S3.2) to ensure a full set of standardized vital rates. Results for the reduced set of standardized vital rates for pre-breeding census models are presented in Fig. S3.15 and Fig. S3.16. To avoid bounding problems when imputing vital rates, we log-transformed fecundity and used a logit transformation for survival and maturation rates. For early maturation species, maturation rate was $m = 1$ and this value was adjusted to $m = 0.999$ prior to transformation.

We combined the standardized vital rates with avian body mass and life history trait data from a database of amniote life history traits (Myhrvold et al. 2015) and from EltonTraits 1.0 (Wilman et al. 2014), a database of foraging attributes for birds and mammals. Both databases contained adult body mass data so we used the mean of these values. We chose female age at maturity and clutch size to characterize life history because we expected these traits to covary with vital rates (Ricklefs 2000, Sæther and Bakke 2000). We log-transformed body mass and age at maturity and we used a square root transformation of clutch size to ensure the data were approximately normally distributed, as required by the phylogenetic imputation model.

We used `taxize` (version 0.9.94, Chamberlain and Szöcs 2013) to obtain species identifiers from the Integrated Taxonomic Information System (ITIS) (http://www.itis.gov) and used these identifiers to combine the standardized vital rates, body mass, and life history trait data. We created three trait datasets: standardized vital rates only; standardized vital rates and body mass data; and standardized vital rates, body mass, and life history trait data. Where body mass or life history trait data were not available for a given species, we excluded that species from the corresponding trait dataset so that the datasets used for imputation contained a complete set of values for these traits (Table S3.2).

Table S3.2: Species included in the imputation analysis. References indicate sources for the demographic data. Unless otherwise indicated, data for the species were included in all of the trait datasets and in both pre-breeding and post-breeding census analyses.

Species	Common name	Order	Source
Accipiter nisus	Eurasian sparrowhawk	Accipitriformes	Sæther and Bakke (2000)
Actitis hypoleucos	Common sandpiper	Charadriiformes	Sæther and Bakke (2000)
Actitis macularius	Spotted sandpiper	Charadriiformes	Sæther and Bakke (2000)
Alcedo atthis	Common kingfisher	Coraciiformes	Sæther and Bakke (2000)
Amazona vittata[a,1,2]	Puerto Rican parrot	Psittaciformes	Salguero-Gómez et al. (2016)
Anas fulvigula[a]	Mottled duck	Anseriformes	Salguero-Gómez et al. (2016)
Anser anser[b]	Greylag goose	Anseriformes	Salguero-Gómez et al. (2016)
Anthropoides paradiseus[a]	Blue crane	Gruiformes	Salguero-Gómez et al. (2016)
Anthus pratensis	Meadow pipit	Passeriformes	Sæther and Bakke (2000)
Aphelocoma coerulescens	Scrub jay	Passeriformes	Sæther and Bakke (2000)
Aptenodytes patagonicus	King penguin	Sphenisciformes	Sæther and Bakke (2000)
Aythya affinis[a]	Lesser scaup	Anseriformes	Salguero-Gómez et al. (2016)
Bonasa umbellus[b]	Ruffed grouse	Galliformes	Salguero-Gómez et al. (2016)
Bostrychia hagedash[a,1,2]	Hadeda ibis	Pelecaniformes	Salguero-Gómez et al. (2016)
Calidris temminckii	Temminck's stint	Charadriiformes	Sæther and Bakke (2000)
Calonectris borealis	Cory's shearwater	Procellariiformes	Sæther and Bakke (2000)
Calyptorhynchus lathami[b]	Glossy black cockatoo	Psittaciformes	Salguero-Gómez et al. (2016)
Chen caerulescens	Snow goose	Anseriformes	Sæther and Bakke (2000)
Cyanistes caeruleus	Blue tit	Passeriformes	Sæther and Bakke (2000)

Cygnus olor	Mute swan	Anseriformes	Sæther and Bakke (2000)
Delichon urbicum	Common house martin	Passeriformes	Sæther and Bakke (2000)
Falco peregrinus[b]	Peregrine falcon	Falconiformes	Salguero-Gómez et al. (2016)
Ficedula hypoleuca	European pied flycatcher	Passeriformes	Sæther and Bakke (2000)
Fratercula arctica	Atlantic puffin	Charadriiformes	Sæther and Bakke (2000)
Fulmarus glacialis	Northern fulmar	Procellariiformes	Sæther and Bakke (2000)
Geospiza conirostris[1,2]	Large cactus finch	Passeriformes	Sæther and Bakke (2000)
Geospiza fortis[1,2]	Medium ground finch	Passeriformes	Sæther and Bakke (2000)
Gymnorhinus cyanocephalus	Pinyon jay	Passeriformes	Sæther and Bakke (2000)
Gyps coprotheres[b]	Cape vulture	Accipitriformes	Salguero-Gómez et al. (2016)
Hylocichla mustelina	Wood thrush	Passeriformes	Sæther and Bakke (2000)
Jynx torquilla[a]	Wryneck	Piciformes	Salguero-Gómez et al. (2016)
Lagopus muta[a]	Japanese rock ptarmigan	Galliformes	Salguero-Gómez et al. (2016)
Megadyptes antipodes	Yellow-eyed penguin	Sphenisciformes	Sæther and Bakke (2000)
Megascops asio	Eastern screech-owl	Strigiformes	Sæther and Bakke (2000)
Melanerpes formicivorus	Acorn woodpecker	Piciformes	Sæther and Bakke (2000)
Melospiza melodia	Song sparrow	Passeriformes	Sæther and Bakke (2000)
Milvus migrans[a]	Black kite	Accipitriformes	Salguero-Gómez et al. (2016)
Morus bassanus	Northern gannet	Suliformes	Sæther and Bakke (2000)
Pernis apivorus[a]	European honey buzzard	Accipitriformes	Salguero-Gómez et al. (2016)
Petrochelidon pyrrhonota	Cliff swallow	Passeriformes	Sæther and Bakke (2000)
Phalacrocorax aristotelis	European shag	Suliformes	Sæther and Bakke (2000)
Pluvialis apricaria	European golden plover	Charadriiformes	Sæther and Bakke (2000)

Pygoscelis adeliae	Adelie penguin	Sphenisciformes	Sæther and Bakke (2000)
Rissa tridactyla	Black-legged kittiwake	Charadriiformes	Sæther and Bakke (2000)
Setophaga discolor[1]	Prairie warbler	Passeriformes	Sæther and Bakke (2000)
Stercorarius maccormicki[1]	South polar skua	Charadriiformes	Sæther and Bakke (2000)
Stercorarius parasiticus	Arctic skua	Charadriiformes	Sæther and Bakke (2000)
Strix occidentalis	Spotted owl	Strigiformes	Sæther and Bakke (2000)
Thalassarche melanophris[a,1]	Black-browed albatross	Procellariiformes	Salguero-Gómez et al. (2016)
Zonotrichia leucophrys	White-crowned sparrow	Passeriformes	Sæther and Bakke (2000)

a. Pre-breeding census model; b. Post-breeding census model

1. Standardized vital rate data; 2. Standardized vital rate + body mass data.

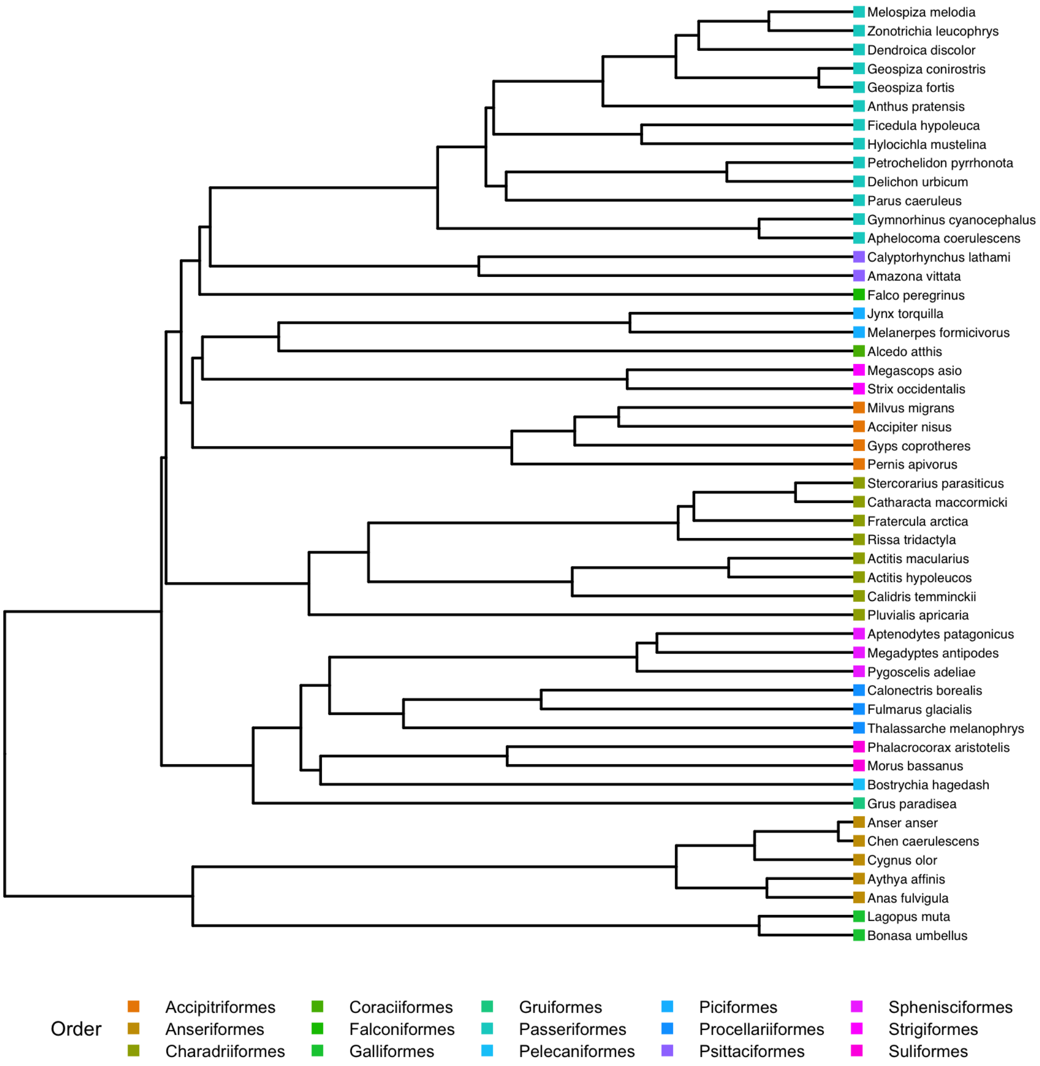

Figure S3.3: Least squares consensus phylogenetic tree for the species included in the analysis, generated from a sample of 1000 phylogenetic trees from BirdTree (www.birdtree.org, Jetz et al. 2012) and visualised using the `ggtree` package (version 2.0.4, Yu et al. 2017, 2018).

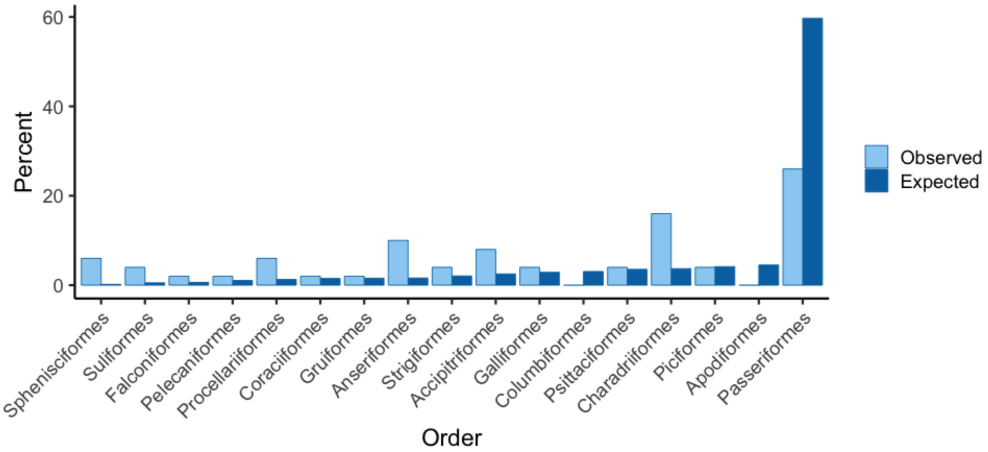

Figure S3.4: Taxonomic bias for the species included in the analysis. Light bars represent the observed percentage of species in each taxonomic order while dark bars show the expected percentage of species based on the taxonomic species richness. Orders in which no species were observed are included only if at least one species was expected.

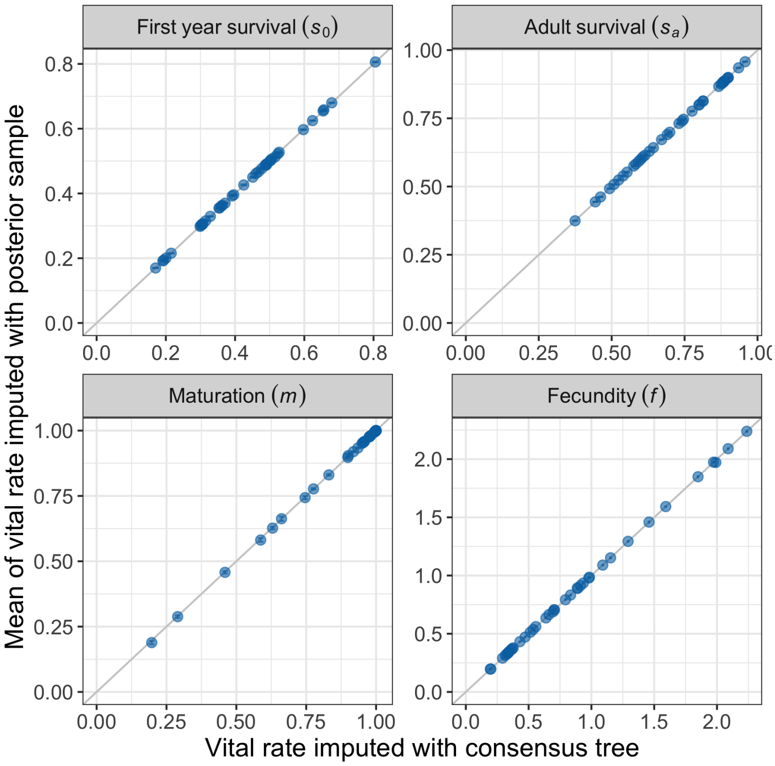

Figure S3.5: Imputation of single vital rates across a sample of 50 trees from the posterior distribution accorded well with the results for the consensus tree, demonstrating that phylogenetic uncertainty is not likely to impact the results of our analysis. Points and error bars indicate the mean and standard error across the posterior sample.

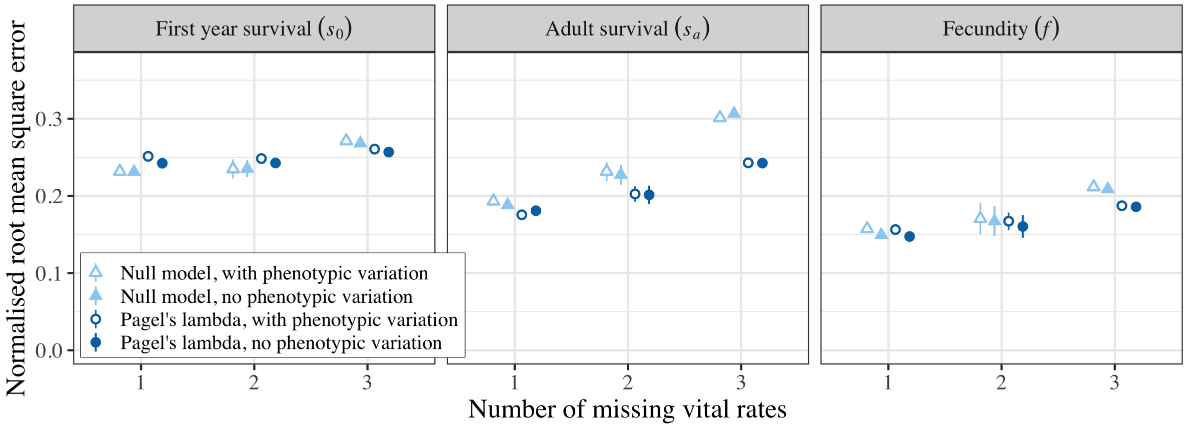

Figure S3.6: Normalised root mean square imputation error for vital rates imputed with different numbers of missing vital rates, with (open symbols) and without (filled symbols) phenotypic variation, for post-breeding census model standardized vital rate data. Each column corresponds to the focal vital rate. Shape indicates whether imputation was carried out under a null (triangle) or Pagel's λ (circle) phylogenetic model. Points show the mean errors across combinations of the same number of missing vital rates and error bars indicate the range of normalised root mean square error for different missing vital rate combinations.

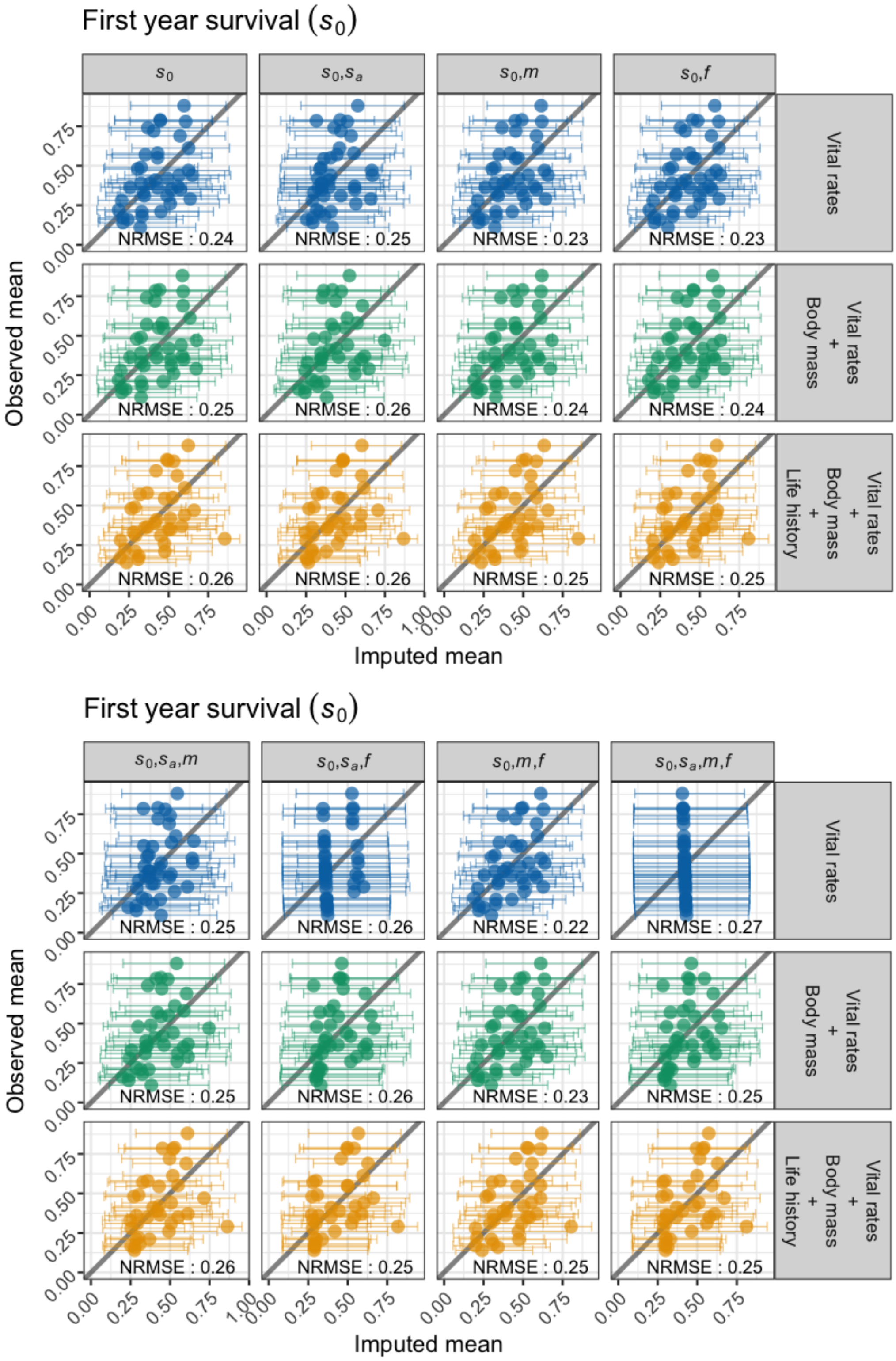

Figure S3.7: Observed first year survival (s_0) for post-breeding census models against values imputed under the null model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

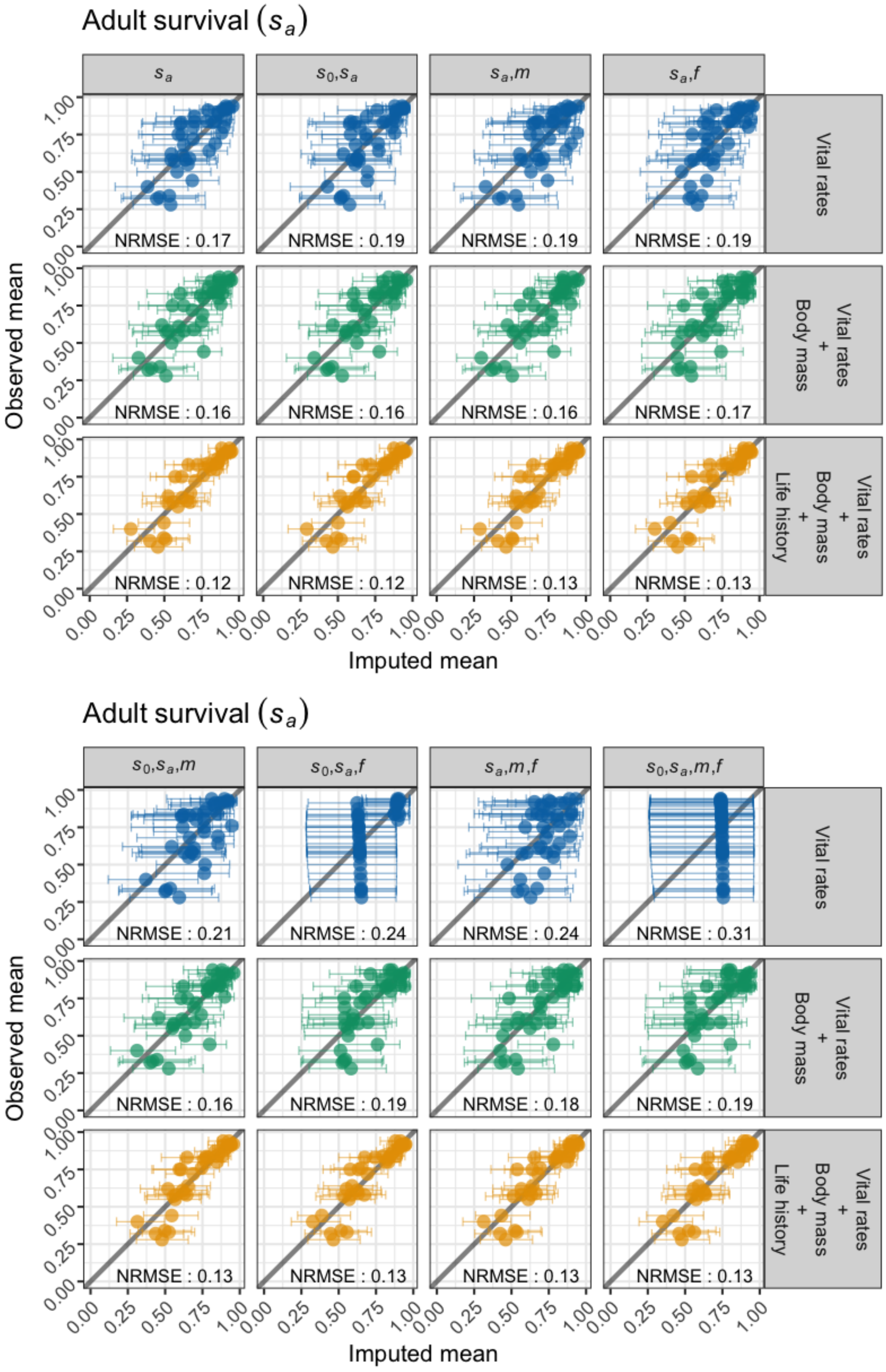

Figure S3.8: Observed adult survival (s_a) for post-breeding census models against values imputed under the null model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

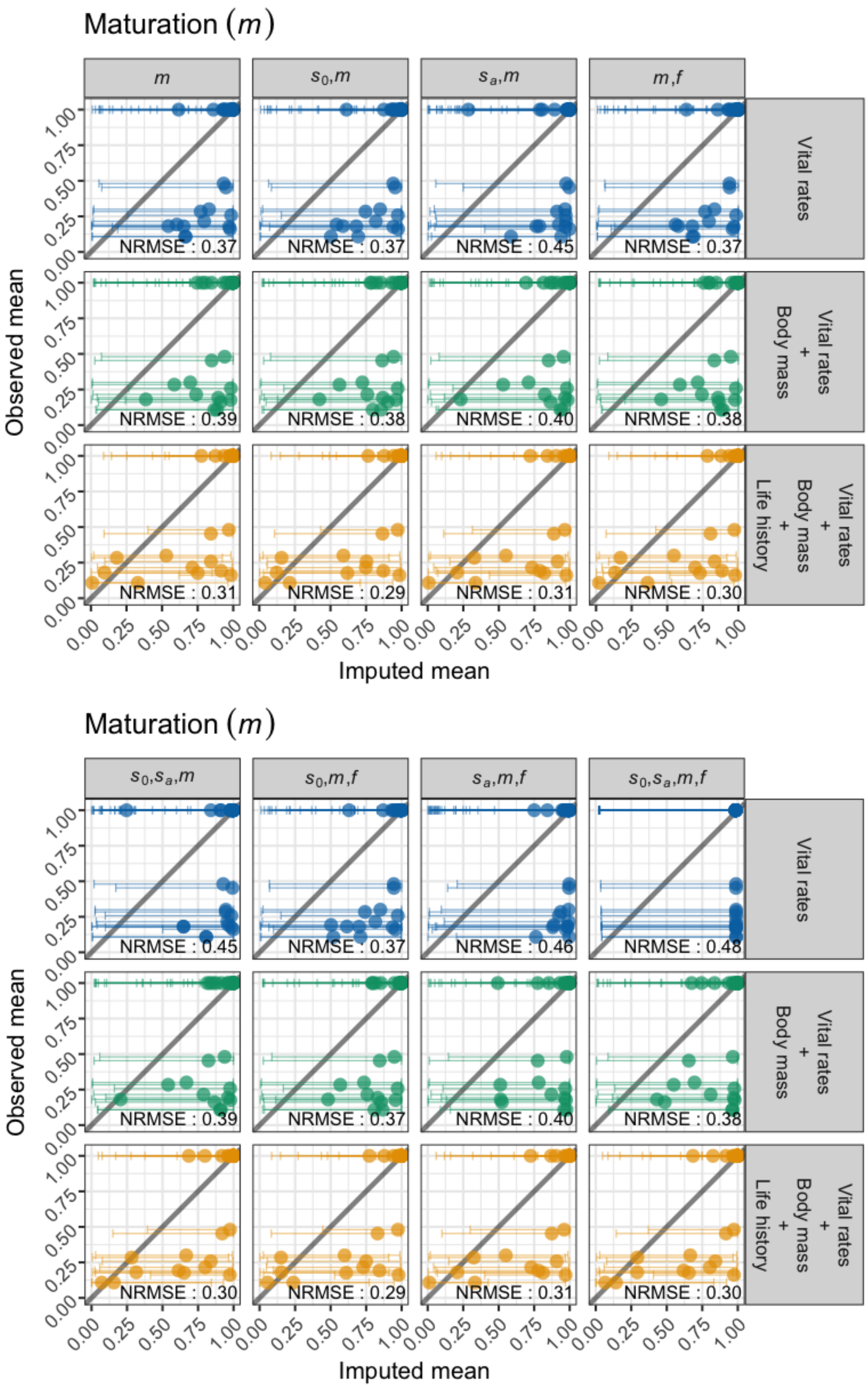

Figure S3.9: Observed maturation rate (m) for post-breeding census models against values imputed under the null model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

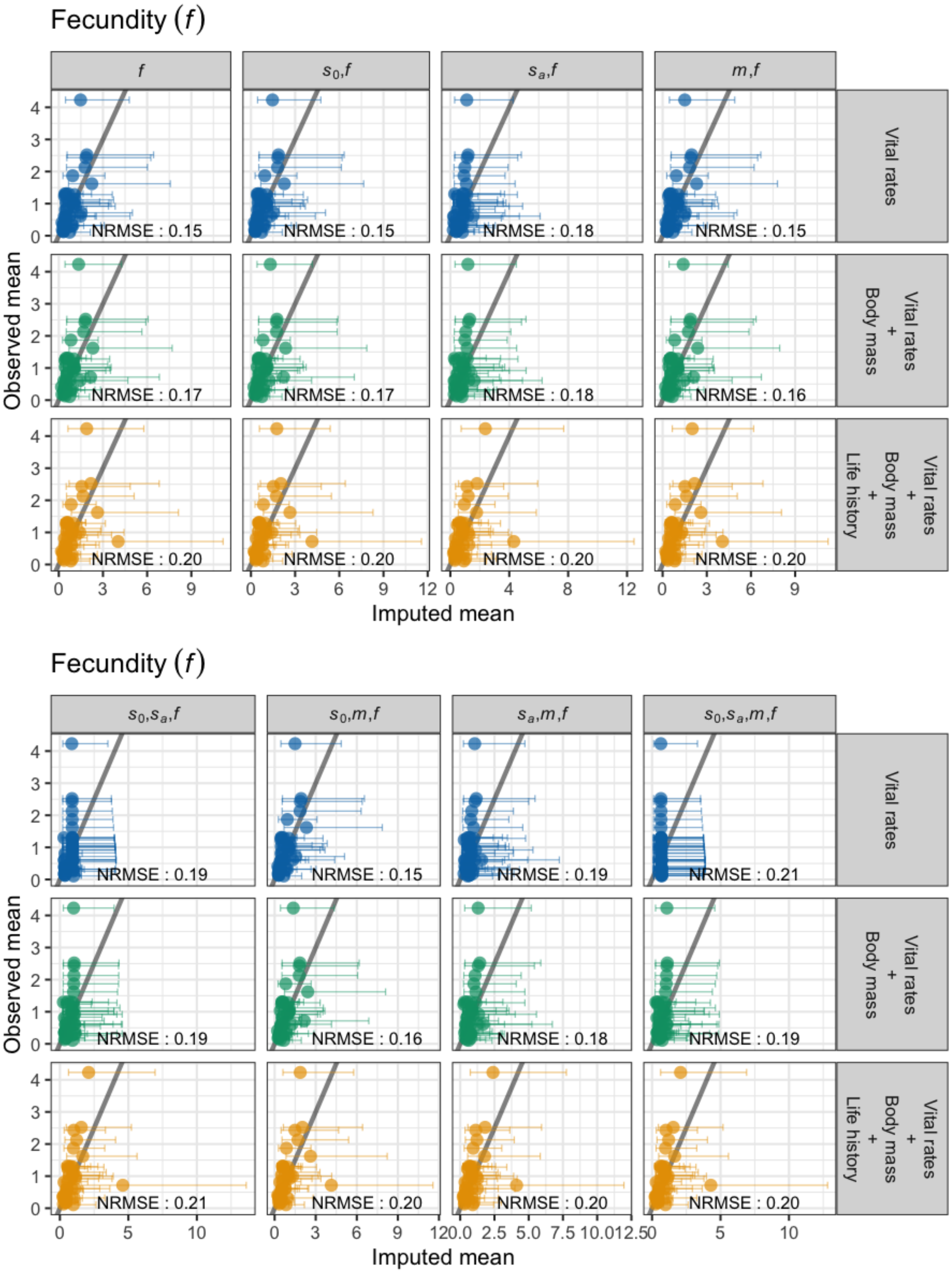

Figure S3.10: Observed fecundity (f) for post-breeding census models against values imputed under the null model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

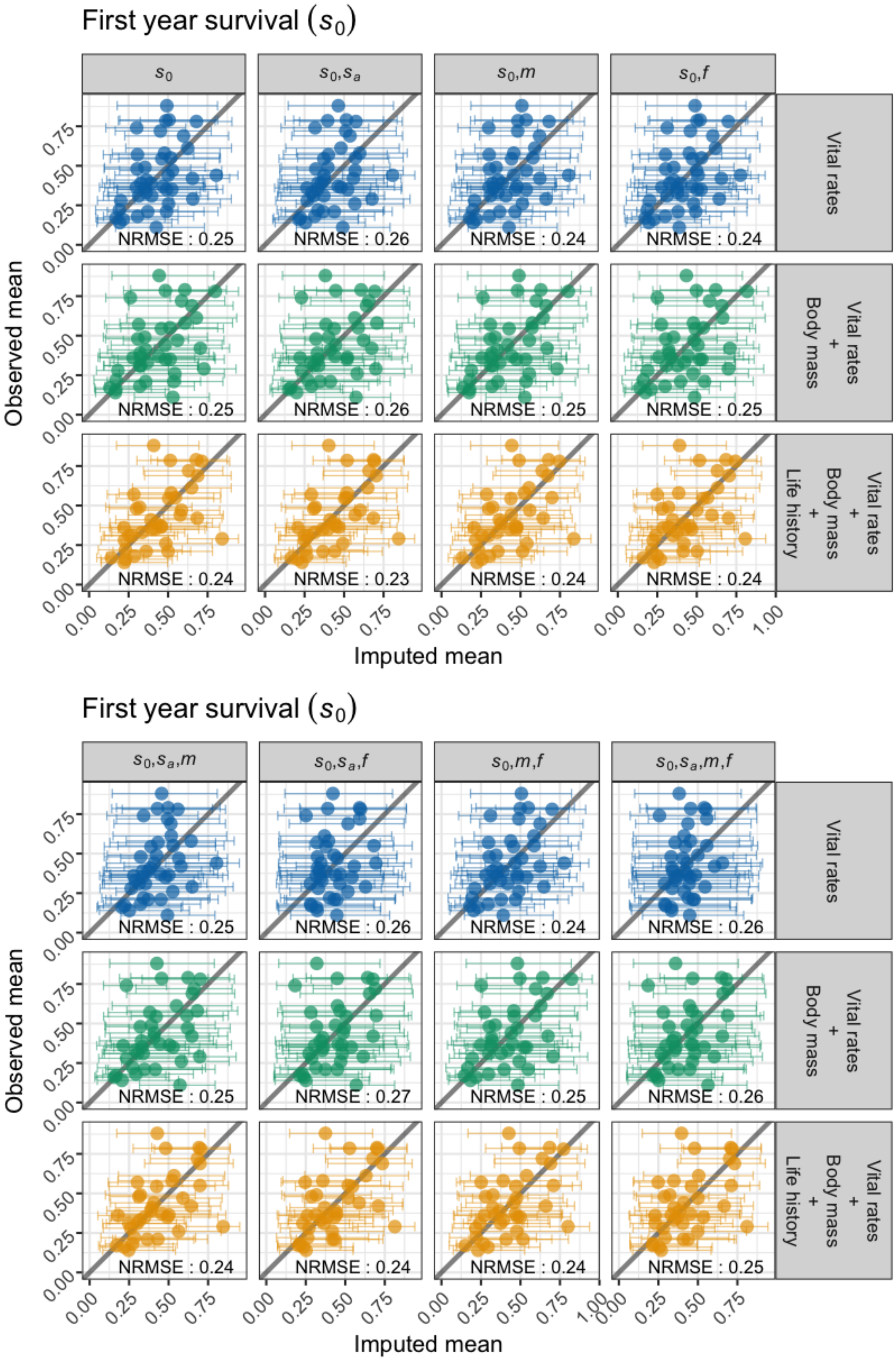

Figure S3.11: Observed first year survival (s_0) for post-breeding census models against values imputed under a Pagel's λ model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

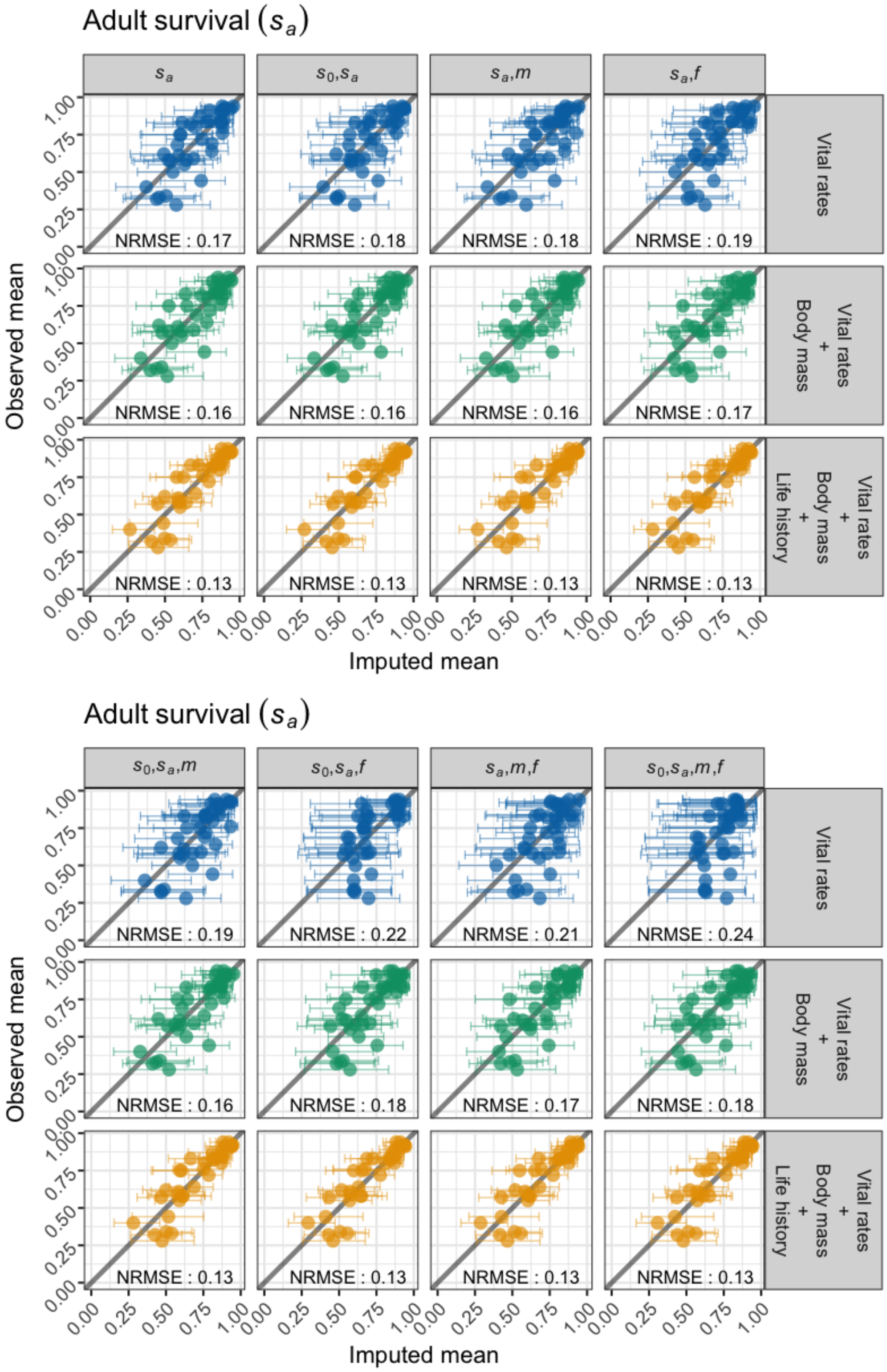

Figure S3.12: Observed adult survival (s_a) for post-breeding census models against values imputed under a Pagel's λ model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

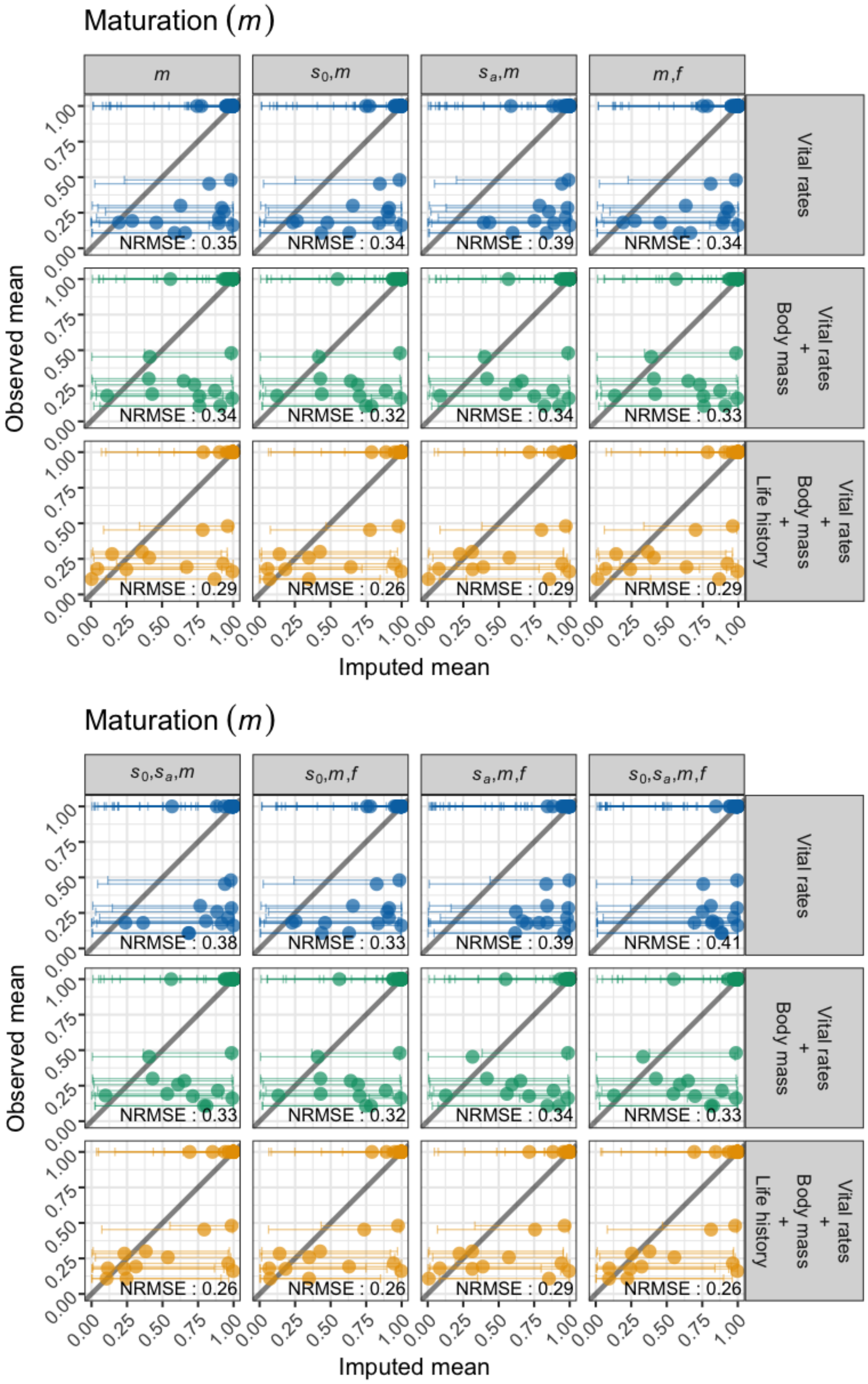

Figure S3.13: Observed maturation rate (m) for post-breeding census models against values imputed under a Pagel's λ model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

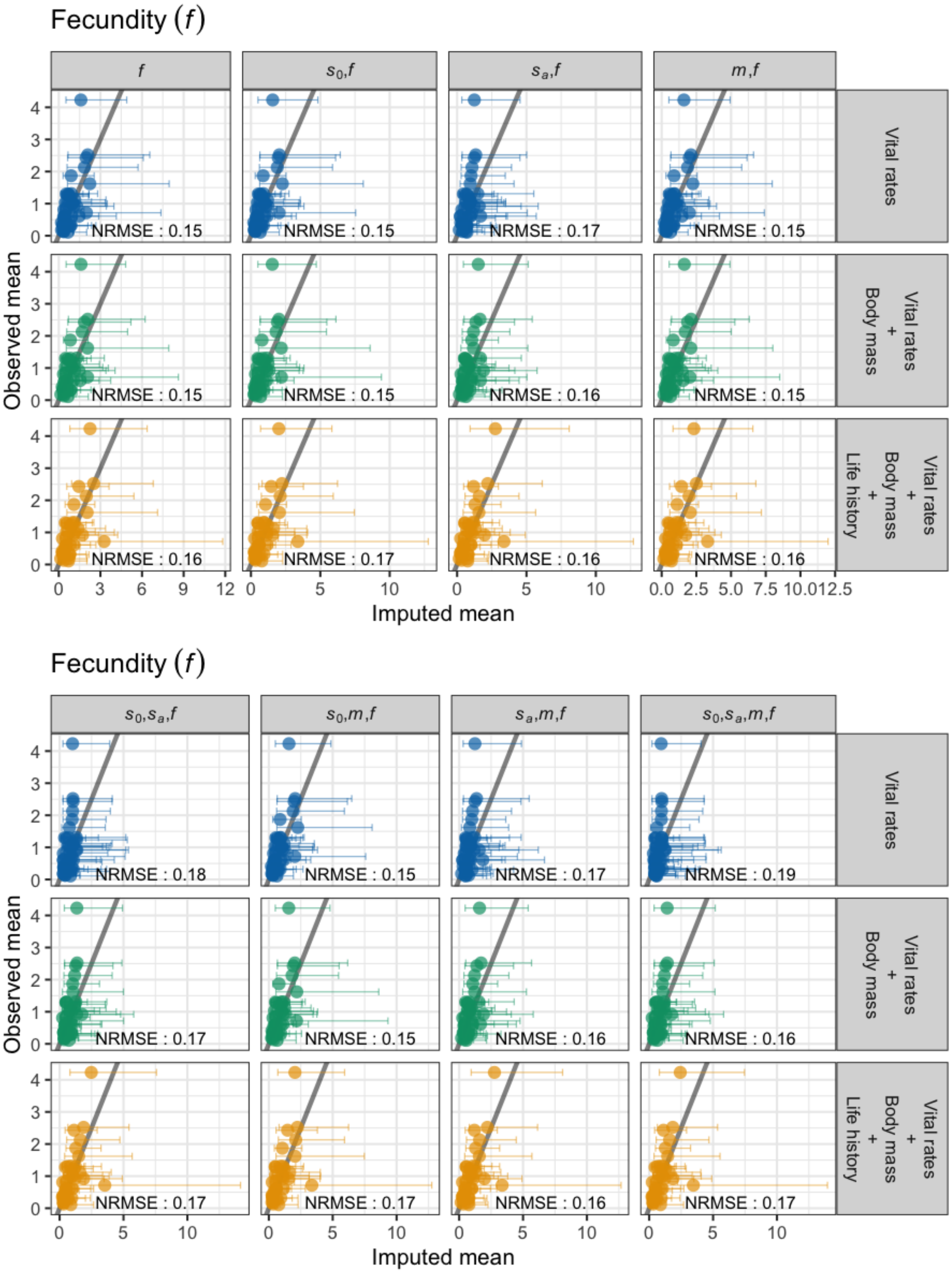

Figure S3.14: Observed fecundity (f) for post-breeding census models against values imputed under a Pagel's λ model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

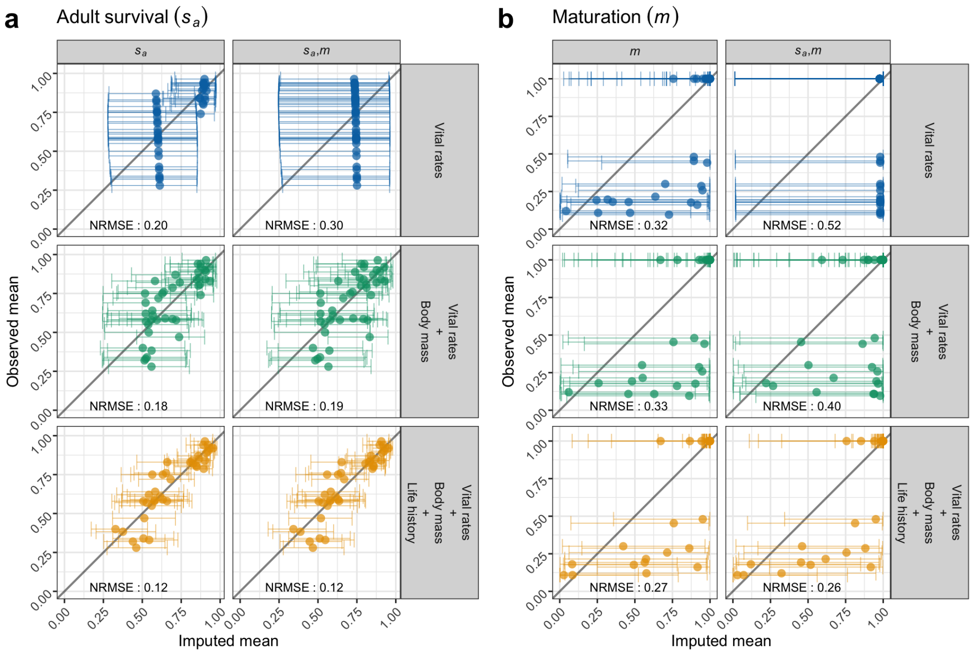

Figure S3.15: Observed (a) adult survival (s_a) and (b) maturation rate (m) for pre-breeding census models against values imputed under the null model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: adult survival (s_a), maturation rate (m). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

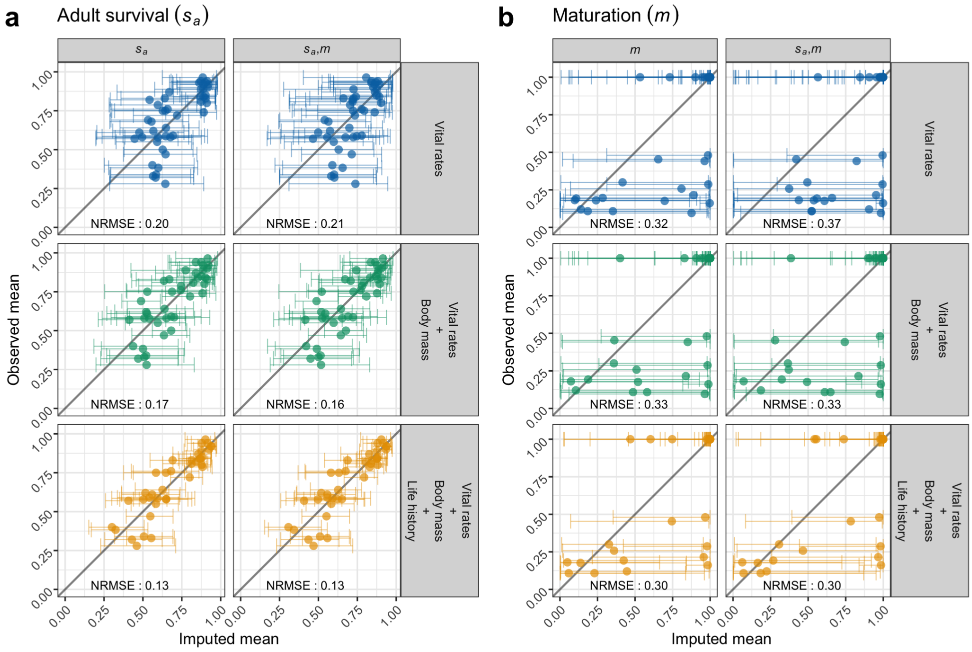

Figure S3.16: Observed (a) adult survival (s_a) and (b) maturation rate (m) for pre-breeding census models against values imputed under a Pagel's λ model. Error bars show 95% confidence intervals for the imputed values. Each column corresponds to a different set of missing vital rates: adult survival (s_a), maturation rate (m). Rows indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

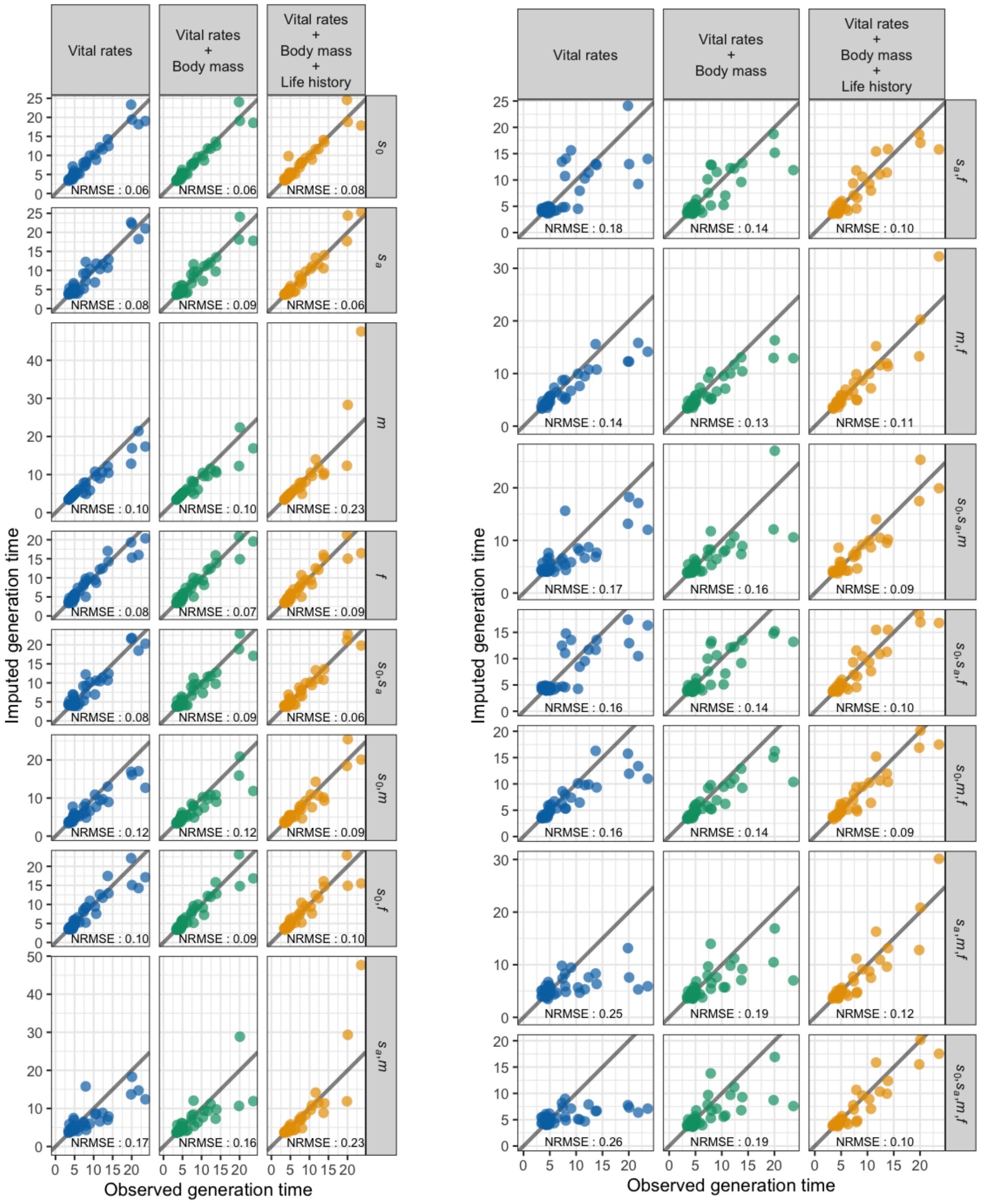

Figure S3.17: Generation time calculated from a model with one or more imputed vital rate against generation time calculated using the original vital rates. Each row corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Columns indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values. Maturation rate was under-estimated for Cory's shearwater (*Calonectris borealis*) and King penguin (*Aptenodytes patagonicus*) when life history traits were included, driving over-estimation of generation time.

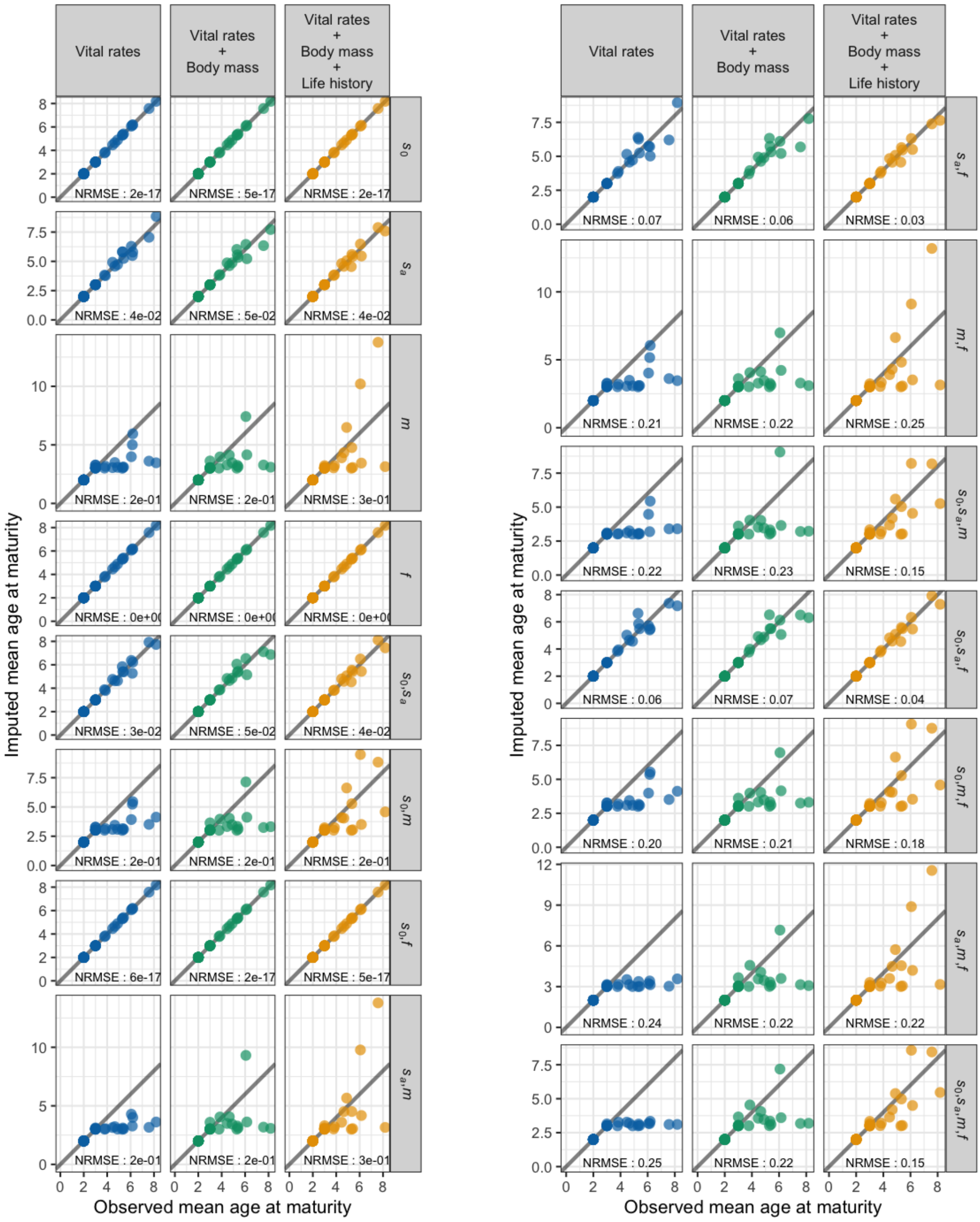

Figure S3.18: Mean age at maturity calculated from a model with one or more imputed vital rate against mean age at maturity calculated using the original vital rates. Each row corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Columns indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values. Maturation rate was under-estimated for Cory's shearwater (*Calonectris borealis*) and King penguin (*Aptenodytes patagonicus*) when life history traits were included, driving over-estimation of mean age at maturity.

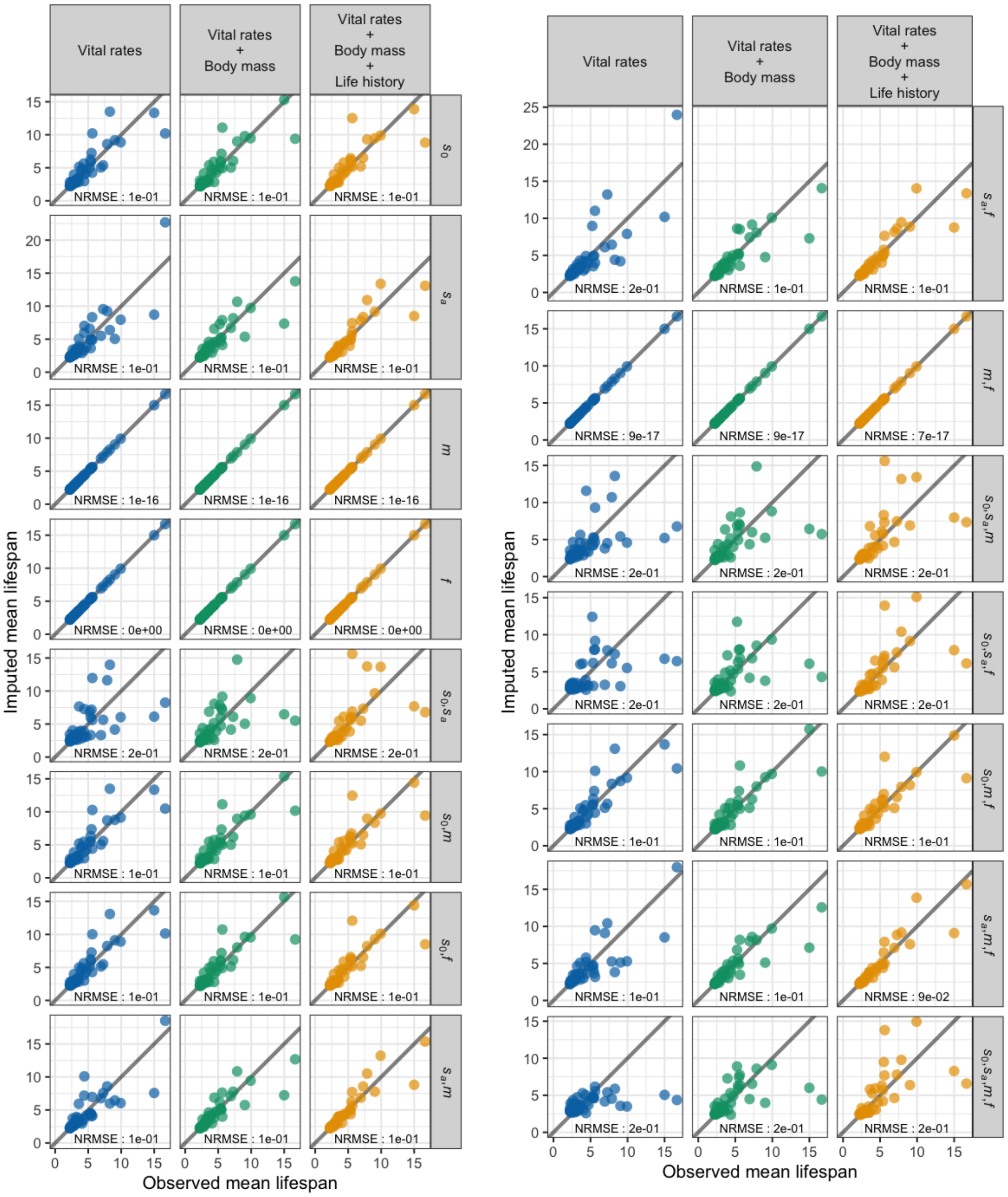

Figure S3.19: Mean lifespan calculated from a model with one or more imputed vital rate against mean lifespan calculated using the original vital rates. Each row corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Columns indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values.

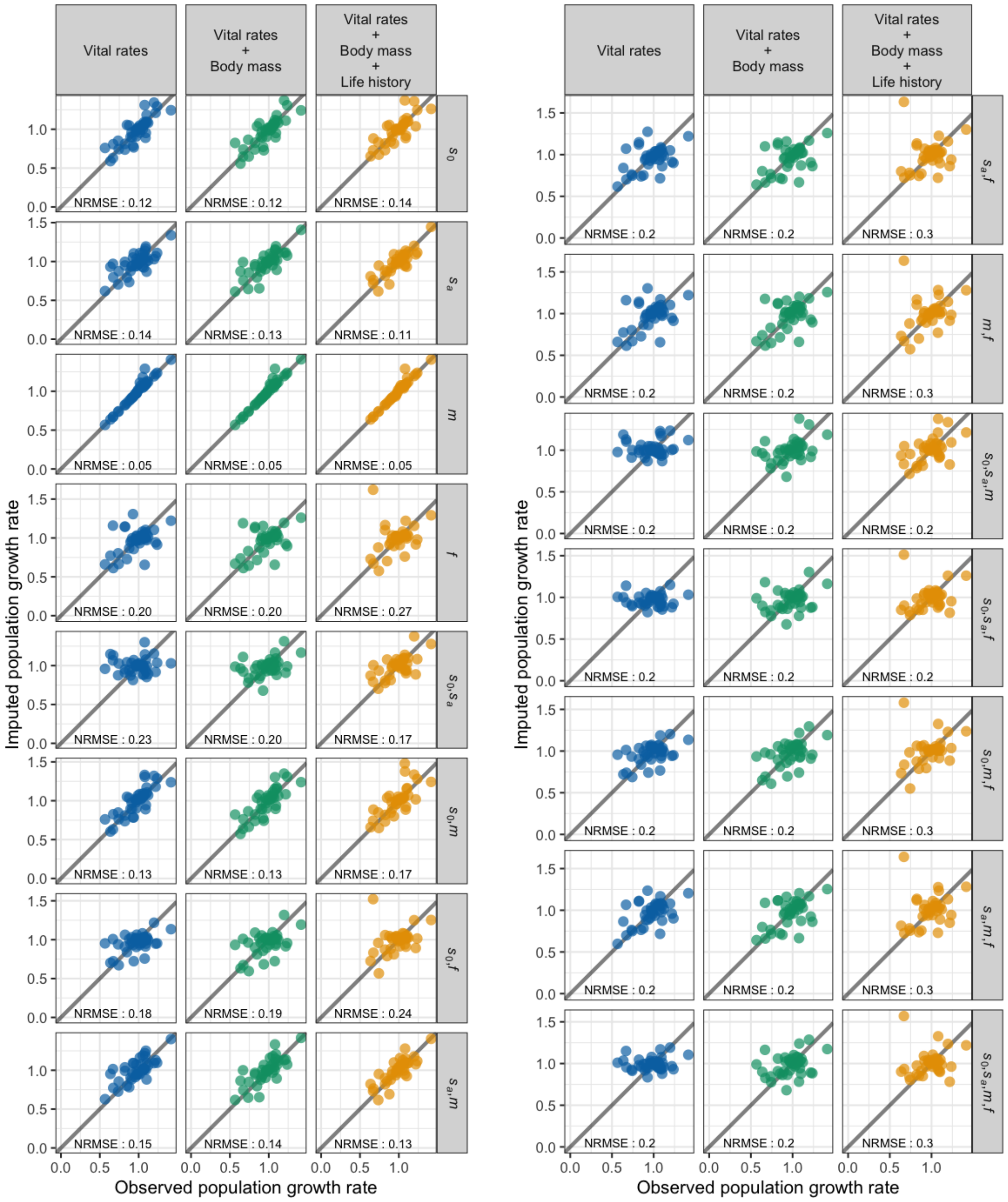

Figure S3.20: Population growth rate calculated from a model with one or more imputed vital rate against population growth rate calculated using the original vital rates. Each row corresponds to a different set of missing vital rates: first year survival (s_0), adult survival (s_a), maturation rate (m), fecundity (f). Columns indicate which trait data were included in the imputation. Imputed values that fall on the grey 1:1 line are identical to the original values. Fecundity was over-estimated for Ruffed grouse (*Bonasa umbellus*) when life history traits were included, driving over-estimation of population growth rate. The original study for this data recorded low fecundity and low population growth rate, but notes that the population is likely maintained by cyclic dynamics which are linked to masting events (Tirpak et al. 2006).

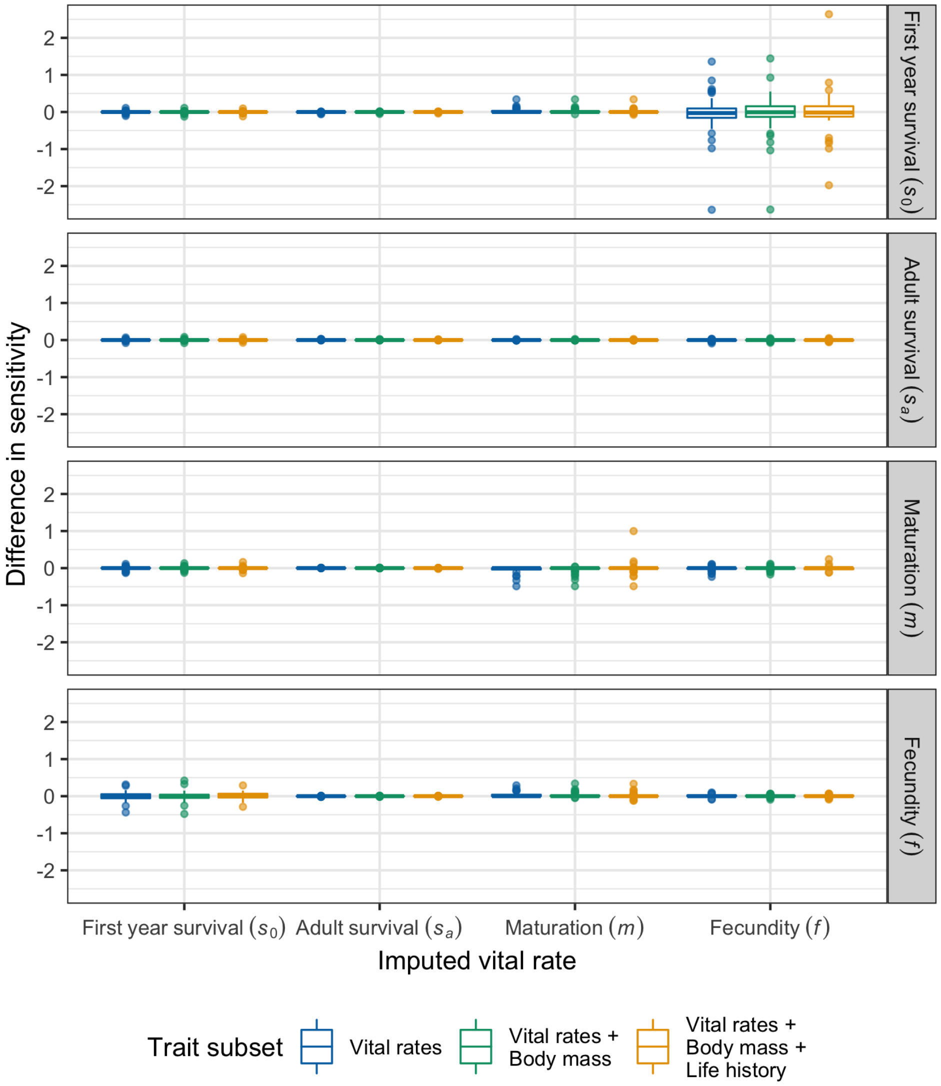

Figure S3.21: Difference in sensitivity of population growth rate to the underlying vital rates calculated using a single imputed vital rate and using the original vital rates. Rows correspond to the vital rate to which sensitivity was calculated. Colour indicates which trait data were included in the imputation.

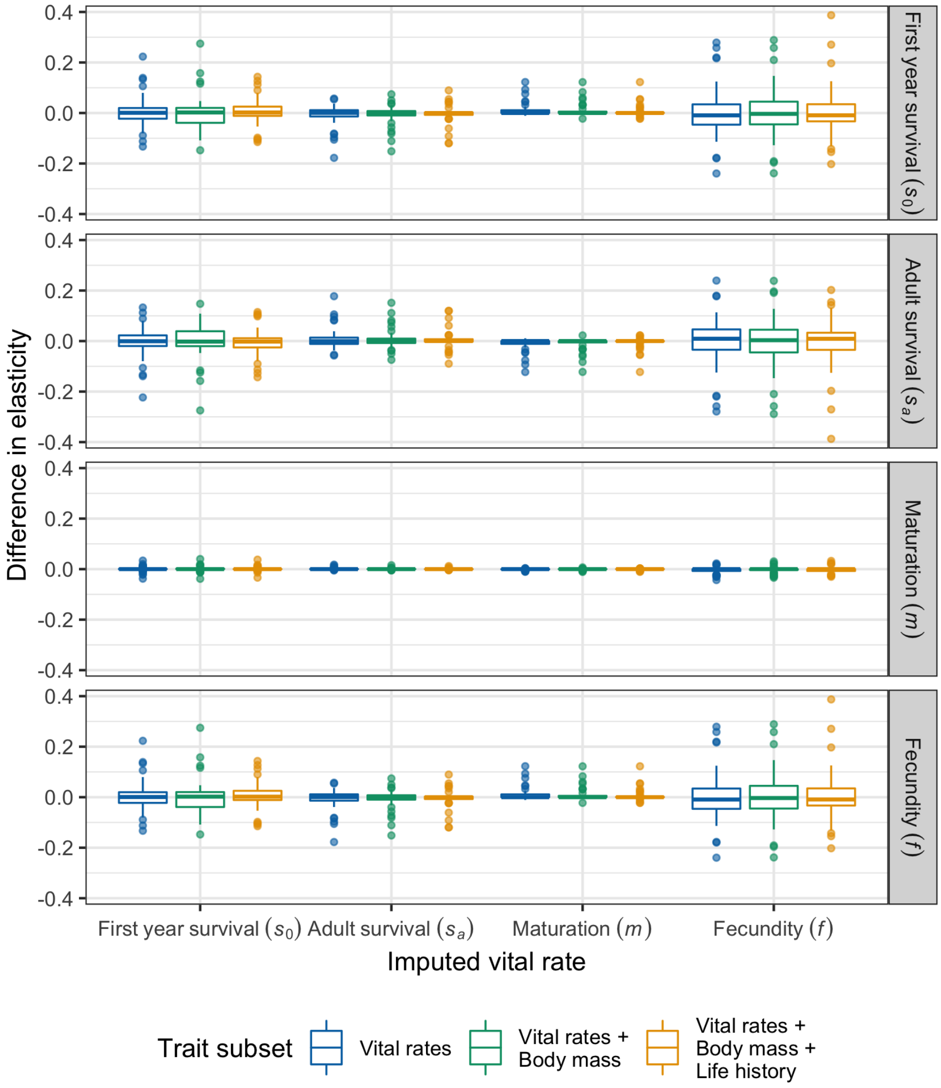

Figure S3.22: Difference in elasticity of population growth rate to the underlying vital rates calculated using a single imputed vital rate and using the original vital rates. Rows correspond to the vital rate to which elasticity was calculated. Colour indicates which trait data were included in the imputation.

Chapter 4

Using pace of life indicators to assess demographic responses to mortality in seabirds

Tamora James, Dylan Childs, Andrew Beckerman

This manuscript is in preparation for submission to *Ecology and Evolution*.

Abstract

1. Managing risks to vulnerable species requires knowledge of demographic responses to threats such as habitat loss, over-exploitation, and climate change. However, the data on growth, survival/mortality, and reproduction (vital rates) required to predict such responses is challenging to acquire. One approach to defining management criteria when the vital rates that underlie demographic models are lacking is to generalise about risk across comparable species using indicators that capture the pace of life.

2. Pace of life indicators use life history traits such as age at maturity, lifespan, and clutch size to place species on a "fast-slow" continuum. Strong links between vital rates and these more easily collected life history traits suggest that indicators that characterise species' pace of life could be used to generalise about population responses to disturbance.

3. We developed a framework in which species' demographic responses to increased mortality are related to two composite pace of life indicators: the major axis of life history trait variation defined by a phylogenetic principal component analysis, and generation length, a metric based on life history traits which captures generational turnover. We applied classical sensitivity and transient analyses within this framework to UK seabird species considered at threat from mortality-generating human activities such as offshore marine developments.

4. We found that the two proxies representing pace of life provided some indication of

demographic responses to elevated mortality risk in seabirds. Elasticity of population growth rate to mortality hazard rate reduced in magnitude as pace of life slowed. Pace of life was not a useful proxy for short-term amplification and attenuation but sensitivity of amplification metrics to mortality hazard rate decreased for slower species. There was a tendency for slower recovery in slow-paced species.

5. Pace of life indicators such as generation length may be a useful proxy for some sensitivities and elasticities of long- and short-term responses to stage-specific changes in vital rates such as mortality. In combination with ecological and behavioural indicators, life history indicators based on pace of life could help in assessing risk to seabirds from extrinsic threats even when direct knowledge of demographic responses is lacking.

Keywords—conservation, demographic modelling, life history, generation time, sensitivity analysis, mortality hazard rate, extinction risk.

4.1 Introduction

Assessing species' vulnerability to impacts from threats such as habitat loss, over-exploitation or climate change is vital for managing natural resources and biodiversity. The mechanisms for such impacts may be complex and indirect (Carslake et al. 2009) and are difficult to measure or predict (Grémillet and Charmantier 2010, Burke et al. 2012). Classical sensitivity and elasticity analyses in conservation focus on the long-term changes to population growth rate arising from perturbations of vital rates such as survival, growth, maturation, and reproductive effort. Complementary to these classical analyses, transient analysis predicts the short-term responses of a population to disturbance or management interventions. These analyses can help to inform the management of vulnerable populations, for example by identifying impacts on vital rates that increase the risk of a population being pushed into decline or by predicting short-term fluctuations in population size that could follow an intervention and be detrimental to population persistence.

However, the estimates of vital rates that underpin these demographic analyses are challenging to acquire, requiring repeated measurements of individuals across many years. In the absence of the detailed data required to conduct such analyses, it is desirable to identify traits that are strongly related to vital rates but for which it is easier to collect data. These proxy traits may reveal patterns that can inform us about long- and short-term population responses to threats. Identifying such patterns among many species may allow us to generalise about the risk that populations will decline or face local extinction due to external threats that influence vital rates.

Life history traits such as clutch size and lifespan are promising candidates for predicting population responses to perturbations due to their close relationship with vital rates such as fecundity and survival. Covariation among life history traits can be used to allocate species to a "fast-slow" continuum that captures pace of life (Stearns 1983, Read and Harvey 1989). Given the close relationship between vital rates and the life history traits which govern species' positions on the fast-slow continuum, pace of life could be used to generalise about population responses to disturbance. For example, in plants, life history traits have been linked to indices of population performance (Salguero-Gómez et al. 2016) and to elasticity of population growth rate to survival, growth, and fecundity (Ramula et al. 2008). These associations suggest that life history traits, which are more easily measured than vital rates, could be used to identify species that are most vulnerable to impacts or to direct management actions towards responsive vital rates (Heppell et al. 2000).

Pace of life indicators rank species along a continuum from "fast" species that are short-lived with high reproductive output and early maturity to "slow" species that are long-lived, mature late and have low reproductive output. For slow species, asymptotic population growth rate typically shows the greatest sensitivity to adult survival (Sæther and Bakke 2000, Oli and Dobson 2003). In these species, constraints on life history mean that adult survival may have a very narrow range of variation (Péron et al. 2016). However, while adult survival may be canalised against environmental variation, anthropogenic factors such as harvesting can have negative impacts on adult survival (Rolland et al. 2010) with significant consequences for long-term population growth rate. Furthermore, although adult survival has the most influence on the population growth rate of species with slow life history, negative impacts on the vital rates of other life stages may also be important to consider when carrying out long-term population projections (Jenouvrier et al. 2005, 2009).

To generate appropriate management criteria, it is important to take into account not only long-term population processes, but also short-term, transient responses to perturbations of population structure (Hastings 2004). Population structure is regularly changed by natural processes (e.g. fires, storms), and in many systems may be affected by anthropogenic factors such as harvesting. Population growth rate is altered by such perturbations in the short term, in a manner that depends on the affected life stages (Koons et al. 2005, Stott et al. 2011). Accounting for these transient dynamics is essential for understanding how populations will respond to disturbance or interventions on the timescales over which conservation typically operates (Ezard et al. 2010, Stott et al. 2012). Transient responses to perturbation can be characterised by indices which describe the magnitude of fluctuations in population density (Stott et al. 2011) and by the damping ratio, a measure of the rate of recovery following disturbance (Caswell 2001). Together, these metrics (Table 4.1) provide a framework that characterises the demographic resilience of a population (Capdevila et al. 2020). As for long-term dynamics, pace of life may be a useful predictor of transient responses.

In this study, we investigate the use of pace of life indicators, representing the fast-slow continuum, to predict the response of population growth rate and transient dynamics to environmental impacts which increase mortality rates. Using pace of life indicators to assess sensitivity to excess mortality could help to identify species which are particularly vulnerable to impacts on the basis of readily available characteristics, even when detailed knowledge of a species' vital rates is lacking. This approach is particularly powerful when responses are evaluated among numerous species. Various composite indicators have been suggested as proxies capturing pace of life, including generation time (Gaillard et al. 2005), ratio of fertility to age at maturity (Oli and Dobson 2003, Stahl and Oli 2006), and principal components (Stearns 1983). Our objective is to identify pace of life proxies suitable for predicting how species will respond to perturbations to mortality rate.

To meet this objective, we consider seabirds, a group of species which are exposed to multiple threats associated with excess mortality due to human activities, such as fisheries bycatch, overfishing, offshore development and environmental pollutants (Dias et al. 2019). Estimating the vulnerability of seabirds to a range of threats has typically focused on ecological characteristics, such as foraging ecology and flight activity (e.g. Furness and Tasker 2000, Garthe and Hüppop 2004, Jones et al. 2008). Here, we shift the focus to life history traits representing the pace of life as a proxy for the vulnerability of marine birds to impacts that increase mortality rates. By exploring patterns among many species along the fast-slow continuum, we hope to generalise about risks to seabirds. Seabirds display a range of life histories along the fast-slow continuum, characterised by differences in lifespan, age at maturity, and clutch size, but with a tendency towards a slow pace of life with relatively low productivity and long lifespan. Differences in their life history traits mean that we expect to see a range of responses to perturbations among seabird species.

Our core analysis explores classical sensitivity of asymptotic population growth rate to stage-specific mortality hazard rate (Ergon et al. 2018). First, we calculate sensitivity and elasticity of population growth rate to stage-specific mortality hazard rate to establish population responses to disturbance across a range of species. We then investigate how these sensitivities and elasticities correlate with two proxy measures of pace of life: the major axis of life history trait variation defined by a phylogenetic principal component analysis (PCA) of traits including age at maturity, longevity, and clutch size; and generation length, a demographic metric derived from age at maturity, lifespan, and survival that describes the rate of replacement of one generation by the next (Gaillard et al. 2005, Bienvenu and Legendre 2015). Furthermore, we seek to identify patterns in short-term responses to disturbance by relating pace of life to transient dynamics, in particular the magnitude and sensitivity to perturbations of transient variation and recovery rates. Together, these analyses provide insight about which demographic responses could be generalised using pace of life proxies (elasticities of asymptotic population growth rate, sensitivity of transient amplification, damping ratio) and how pace of life indicators could contribute to a robust assessment of the risk of population decline due to threats that affect mortality rates.

4.2 Methods

All analyses were carried out in R (version 4.0.2, R Core Team 2020).

4.2.1 Demographic data and model construction

We used demographic data for seabird species considered at risk from offshore developments in the UK (Horswill and Robinson 2015). Data for 22 species (Table S4.1) met the minimum requirements to construct a matrix population model for our analysis: estimates of juvenile and adult survival, age at recruitment and productivity. We used these estimates and additional demographic data such as incidence of missed breeding to construct for each species a post-reproductive stage-classified model with an annual timestep, one or more juvenile

Amplification	
First time-step amplification (reactivity) $\bar{\rho}_1 = \|\hat{\mathbf{A}}\|_1$	Maximum population growth in first time-step relative to population with stable growth rate
Maximum amplification $\bar{\rho}_{\max} = \max_{t>0} \|\hat{\mathbf{A}}^t\|_1$	Maximum population density relative to population with stable growth rate and the same initial size
Amplified inertia $\bar{\rho}_\infty = \dfrac{\mathrm{v}_{\max}\|\mathbf{w}\|_1}{\mathbf{v}^{\mathrm{T}}\mathbf{w}}$	Upper bound for population density after transient fluctuations relative to population with stable growth rate and the same initial size
Attenuation	
First time-step attenuation $\underline{\rho}_1 = \mathrm{minCS}(\hat{\mathbf{A}})$	Minimum population growth in first time-step relative to population with stable growth rate
Maximum attenuation $\underline{\rho}_{\min} = \min_{t>0} \mathrm{minCS}(\hat{\mathbf{A}}^t)$	Minimum population density relative to population with stable growth rate and the same initial size
Attenuated inertia $\underline{\rho}_\infty = \dfrac{\mathrm{v}_{\min}\|\mathbf{w}\|_1}{\mathbf{v}^{\mathrm{T}}\mathbf{w}}$	Lower bound for population density after transient fluctuations relative to population with stable growth rate and the same initial size
Recovery	
Damping ratio $\rho = \dfrac{\lambda_1}{\|\lambda_2\|}$	Rate of convergence to a stable state, the strength of asymptotic population growth rate relative to transient effects

Table 4.1: Transient metrics of short-term population dynamics are calculated from the standardised matrix population model $\hat{\mathbf{A}} = \mathbf{A}/\lambda_1$ where λ_1 is the dominant eigenvalue (Stott et al. 2011). minCS denotes the minimum column sum of a matrix, $\mathbf{v}$ and $\mathbf{w}$ are the reproductive value and stable stage distribution of $\mathbf{A}$, respectively, and λ_2 is the eigenvalue with the second largest magnitude.

stages and a breeding adult stage (Caswell 2001). The model takes the form

$$\mathbf{A} = \begin{bmatrix} s_1(1-\gamma_1) & 0 & \cdots & s_{m-1}\gamma_{m-1}f & s_m(1-\gamma_m)f \\ s_1\gamma_1 & s_2(1-\gamma_2) & & & 0 \\ 0 & s_2\gamma_2 & \ddots & & \\ \vdots & & \ddots & & \vdots \\ & & & s_{m-1}(1-\gamma_{m-1}) & \\ 0 & 0 & \cdots & s_{m-1}\gamma_{m-1} & s_m(1-\gamma_m) \end{bmatrix}, \tag{4.1}$$

where s_k and γ_k are the survival rate and transition rate for stage k individuals respectively, f is the per-capita fecundity rate, and m is the number of stages. The transition rate,

$$\gamma_k = \frac{\left(\frac{s_k}{\lambda}\right)^{d_k} - \left(\frac{s_k}{\lambda}\right)^{d_k-1}}{\left(\frac{s_k}{\lambda}\right)^{d_k-1}} \tag{4.2}$$

for stage duration d_k and population growth rate λ, was calculated iteratively until convergence of λ, the dominant eigenvalue of the projection matrix $\mathbf{A}$. We determined the duration of juvenile stages from the age ranges specified for these stages in Horswill and Robinson (2015) and we used maximum longevity from the AnAge database (Tacutu et al. 2018) and the age specified for the adult class in Horswill and Robinson (2015) to estimate adult stage duration.

4.2.2 Asymptotic population growth rate sensitivity analysis

To allow us to analyse the sensitivity and elasticity of asymptotic population growth rate with respect to excess mortality, we reparameterised the matrix population model in terms of time-averaged mortality hazard rate (Ergon et al. 2018):

$$\bar{h}_k = -\log(s_k), \quad k = 1, 2, \ldots m. \tag{4.3}$$

We used the reparameterised model to calculate the sensitivities and elasticities of population growth rate, λ, to mortality hazard rate for each lifecycle stage k. Since the number of juvenile stages varied among species, we retained only the sensitivities and elasticities to mortality hazard rate for the first year (hereafter "juvenile") and adult stages in the subsequent analyses.

4.2.3 Pace of life indicators

We extracted life history trait data (female and male age at maturity, longevity, maximum longevity, and clutch size) from the Amniote database (Myhrvold et al. 2015). We used phylogenetic generalised least squares (pGLS) to obtain body mass residuals for each of the life history traits (Revell 2009) and applied a phylogenetic PCA to the body mass residuals. We used the principal axis of variation, PC1, as a proxy representing pace of life in the subsequent analysis. As a second proxy we used generation length estimates based on published and imputed values for age at first breeding, maximum longevity, and annual adult survival in birds (Bird et al. 2020). To evaluate whether pace of life proxies were effective indicators of the sensitivity and elasticity of population growth rate, λ, to elevated mortality, we tested the hypothesis that sensitivity and elasticity would increase in magnitude as pace of life slowed. We fitted linear models between sensitivity and elasticity of population growth rate to juvenile or adult mortality hazard rate and pace of life. Additionally, we evaluated whether body mass or asymptotic population growth rate, λ, were associated with differences in sensitivity or elasticity to mortality hazard rate by fitting models relating sensitivities and elasticities to body mass (Myhrvold et al. 2015) and to values of λ derived from the matrix population models.

4.2.4 Transient analysis

To evaluate whether pace of life could be used to predict transient responses, we tested the hypothesis that amplification and attenuation metrics and the sensitivity of those metrics to underlying vital rates would be positively related to pace of life proxies. Additionally, we tested the hypothesis that recovery from disturbance, captured by the damping ratio, would be negatively related to pace of life. We used the original vital rates and a series of proportional increases in mortality hazard rate to calculate transient indices of first time-step amplification and attenuation, maximum amplification and attenuation, amplified inertia and attenuated inertia (Table 4.1). For juvenile and adult stages, we increased mortality hazard rate by 10%, 30% or 50% and used the perturbed value, $\bar{h}_k + \Delta\bar{h}_k$, to obtain the difference between the value of each metric $f(\bar{h}_k)$ calculated using original and increased

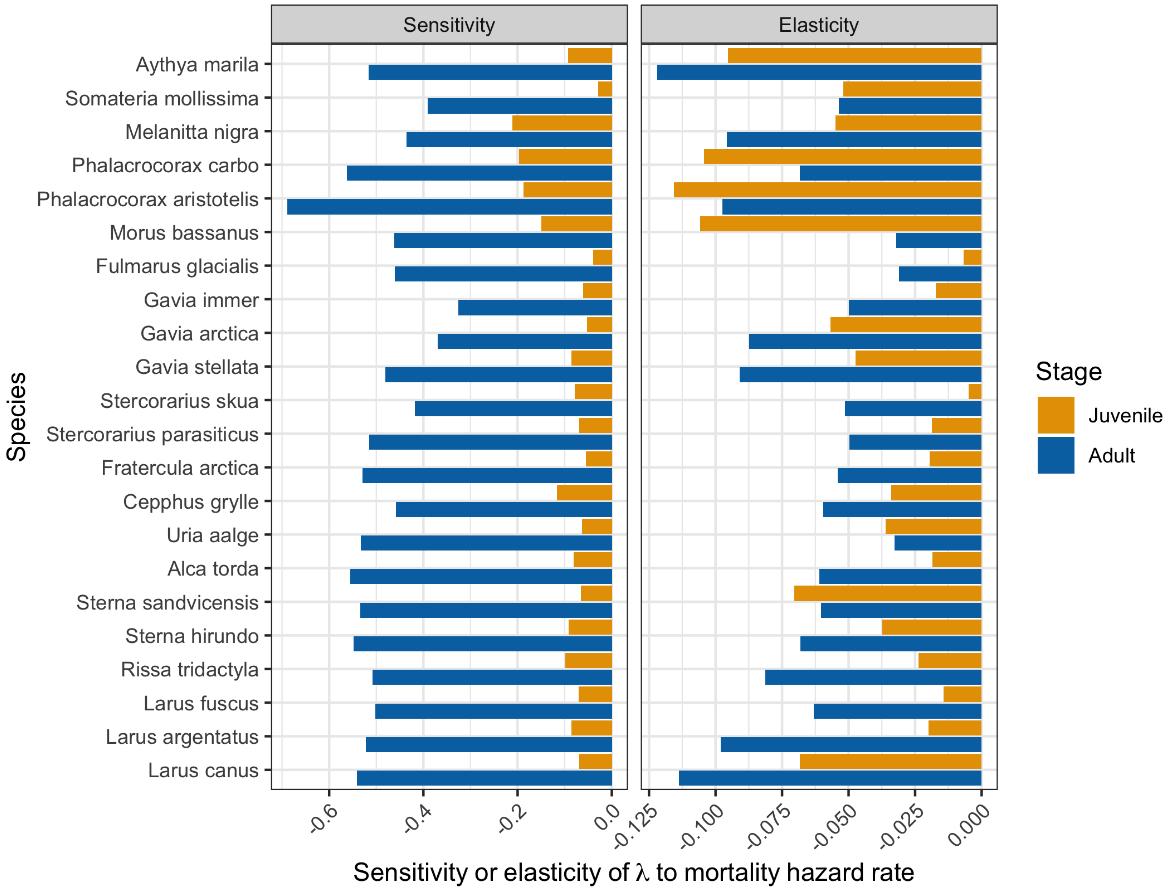

Figure 4.1: Sensitivities of population growth rate, λ, to juvenile and adult mortality hazard rate showed similarities among congenerics, but elasticities were more variable.

juvenile or adult mortality hazard rate:

$$\Delta f_k = f(\bar{h}_k + \Delta\bar{h}_k) - f(\bar{h}_k), \quad k \in \{juv, ad\}. \tag{4.4}$$

We fitted linear models to determine whether the baseline transient indices or the difference in transient indices under perturbation were related to pace of life. We modelled the relationship between damping ratio ρ and pace of life using an inverse Gaussian generalised linear model with an inverse square link function to capture the heavily skewed distribution of damping ratio.

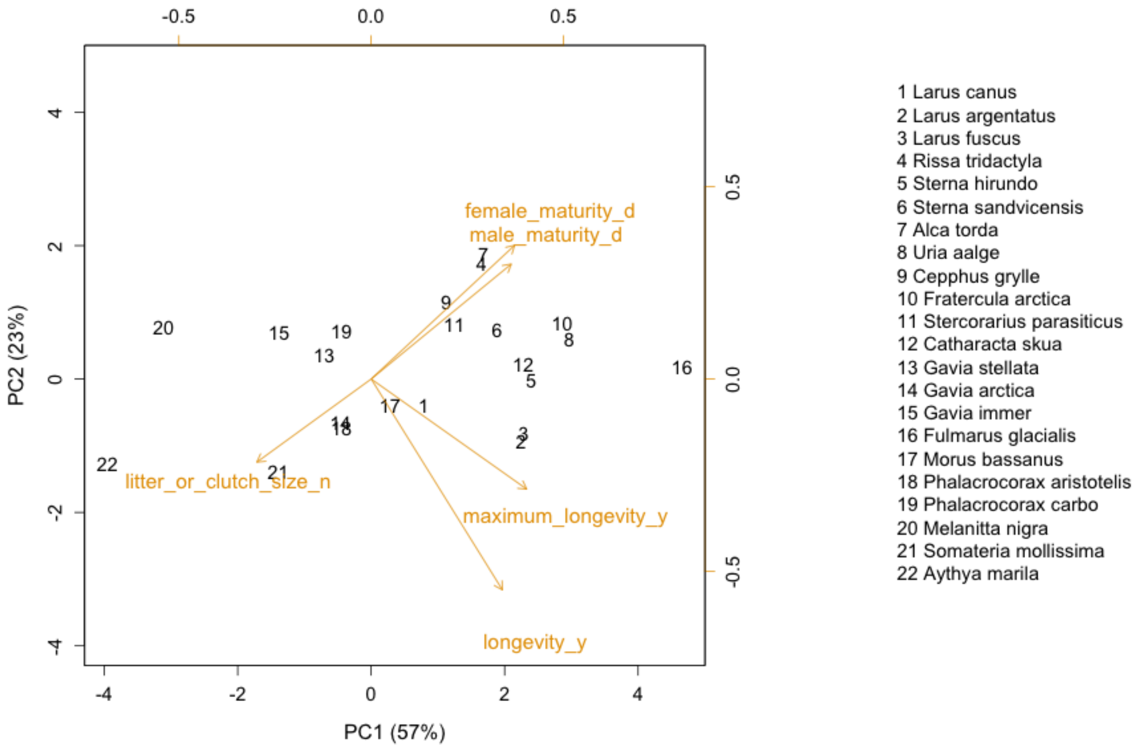

Figure 4.2: Phylogenetically corrected principal component analysis of body mass residuals of life history traits. PC1 explains 57% of the variance and aligns species from “large clutch size, early maturity” to “small clutch size, late maturity”.

4.3 Results

4.3.1 Asymptotic population growth rate sensitivity analysis

Sensitivities and elasticities of asymptotic population growth rate, λ, to mortality hazard rate were always negative, indicating that λ tends to decrease as mortality hazard rate increases (Fig. 4.1). Sensitivities of λ to juvenile and adult mortality hazard rate in related species (e.g. congenerics) had similar magnitudes, but elasticity patterns were more variable. Sensitivity to adult mortality rate was always greater in magnitude than sensitivity to juvenile mortality rate but this was not the case for elasticities to juvenile and adult mortality hazard rate.

4.3.2 Life history proxies

The first principal component (PC1) of the phylogenetic PCA explained 57% of the variance and described an axis of life history variation from species with high fecundity and early maturation ("fast" species) to those with higher age at maturity and lower clutch size ("slow" species), after correcting for body mass and phylogeny (Fig. 4.2). Generation length estimates obtained from Bird et al. (2020) were positively correlated with PC1 estimates (Pearson's $r = 0.76$, $d.f. = 20$, $p < 0.001$), indicating that the two proxies were consistent measures of pace of life.

4.3.3 Relating sensitivity and elasticity to pace of life

To evaluate whether pace of life proxies were useful indicators of the sensitivity and elasticity of population growth rate to increased mortality, we tested the hypothesis that sensitivity and elasticity would be negatively related to pace of life proxies. To assess whether body size or population growth rate influenced sensitivity and elasticity, we also tested the hypothesis that sensitivity and elasticity to mortality hazard rate would be increase in magnitude with body mass and decrease with population growth rate. We found that pace of life and body mass were poor proxies for sensitivity of population growth rate to mortality hazard rate (Fig. 4.3). However, sensitivity to juvenile and adult mortality hazard rate was negatively associated with asymptotic population growth rate, λ ($S_{\bar{h}_{juv}} = 0.40 - 0.50\lambda$, $S_{\bar{h}_{ad}} = -0.07 - 0.43\lambda$, slopes not significantly different, $R^2 = 0.94$).

Pace of life was an effective proxy for elasticity to mortality hazard rate in both juvenile and adult stages. Elasticity to mortality hazard rate was positively associated with PC1 ($E_{\bar{h}_{juv}} = -0.051 + 0.009PC1$, $E_{\bar{h}_{ad}} = -0.075 + 0.007PC1$, $R^2 = 0.46$) and generation length ($E_{\bar{h}_{juv}} = -0.094 + 0.004G$, $E_{\bar{h}_{ad}} = -0.113 + 0.004G$, $R^2 = 0.50$) (Fig. 4.4). Slopes for juvenile and adult mortality hazard rate did not differ significantly in either case. There was no association between elasticity to mortality hazard rate and body mass or population growth rate, λ.

4.3.4 Transient analysis

To determine whether pace of life was a useful proxy for transient responses, we tested the hypothesis that transient indices describing the bounds of amplification and attenuation arising after a structural perturbation and the sensitivity of those metrics to increases in mortality hazard rate would be positively related to pace of life proxies. Additionally, we tested the hypothesis that damping ratio would be negatively related to pace of life. With

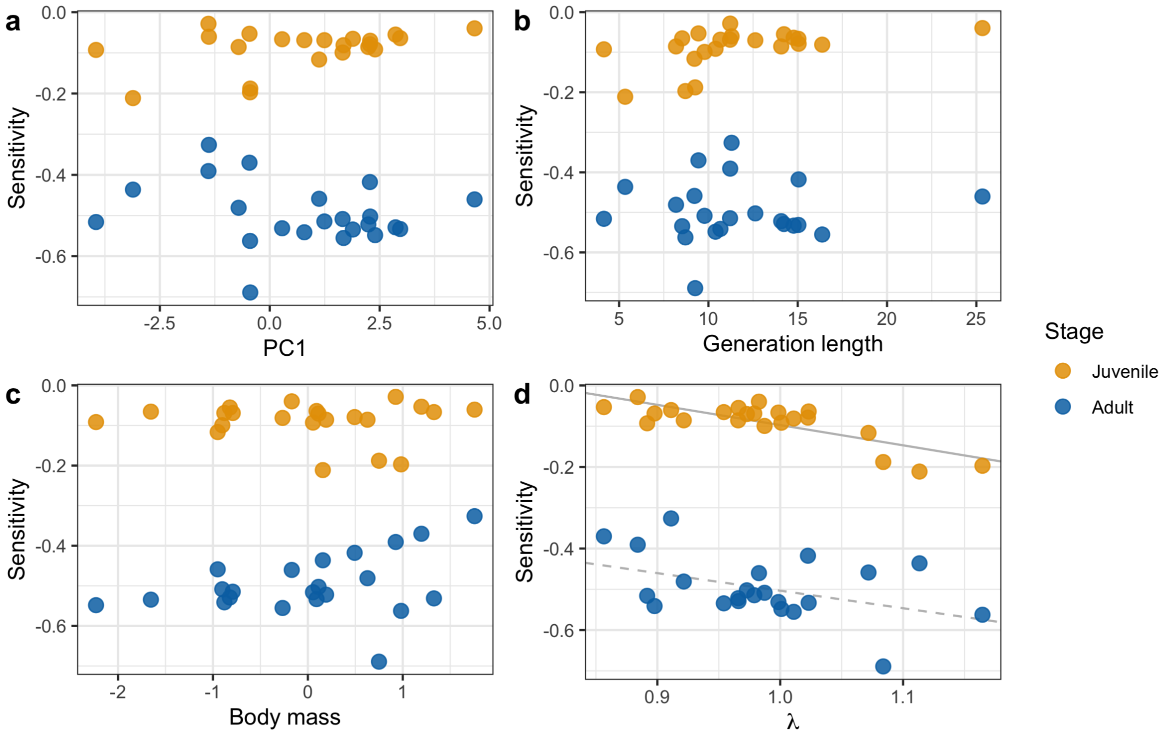

Figure 4.3: Sensitivities of population growth rate to juvenile and adult mortality hazard rates showed a negative relationship with asymptotic population growth rate. Prediction lines indicate support for a relationship between sensitivity to juvenile (solid line) or adult (dashed line) mortality hazard rate and the independent variable: a) PC1, b) generation length, c) body mass, and d) population growth rate, λ.

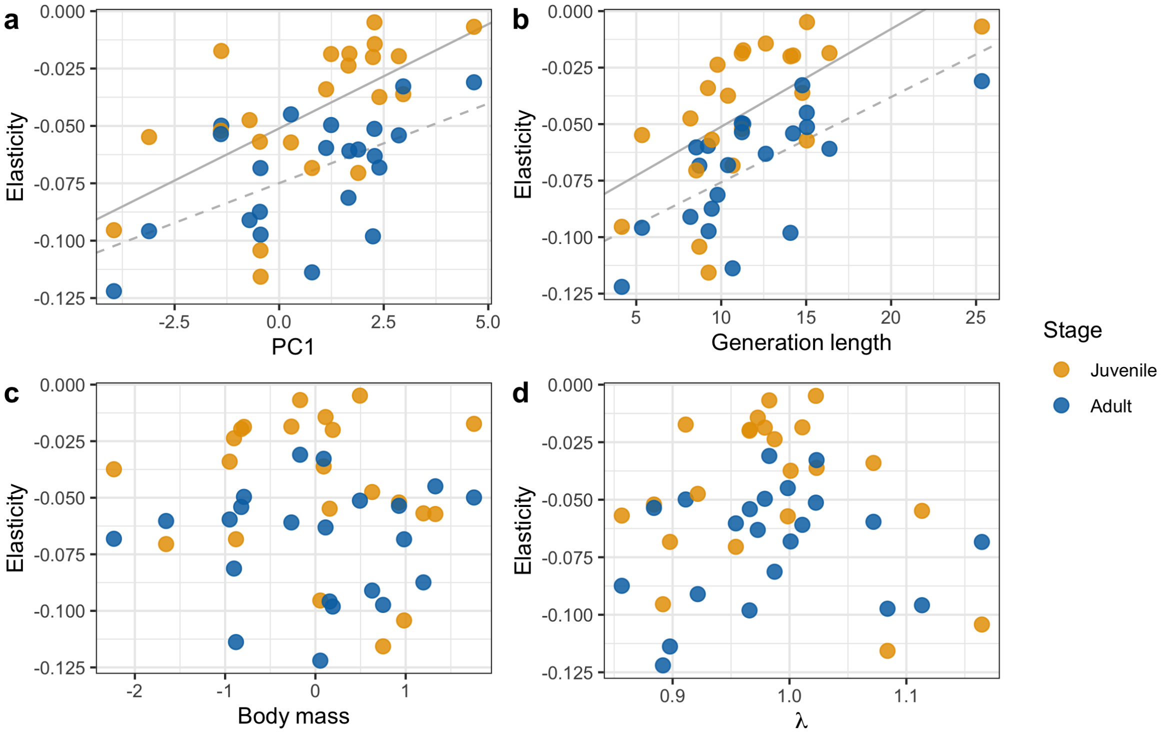

Figure 4.4: Elasticities of population growth rate to juvenile and adult mortality hazard rates showed a positive relationship with pace of life proxies. Prediction lines indicate support for a relationship between elasticity to juvenile (solid line) or adult (dashed line) mortality hazard rate and the independent variable: a) PC1, b) generation length, c) body mass, and d) population growth rate, λ.

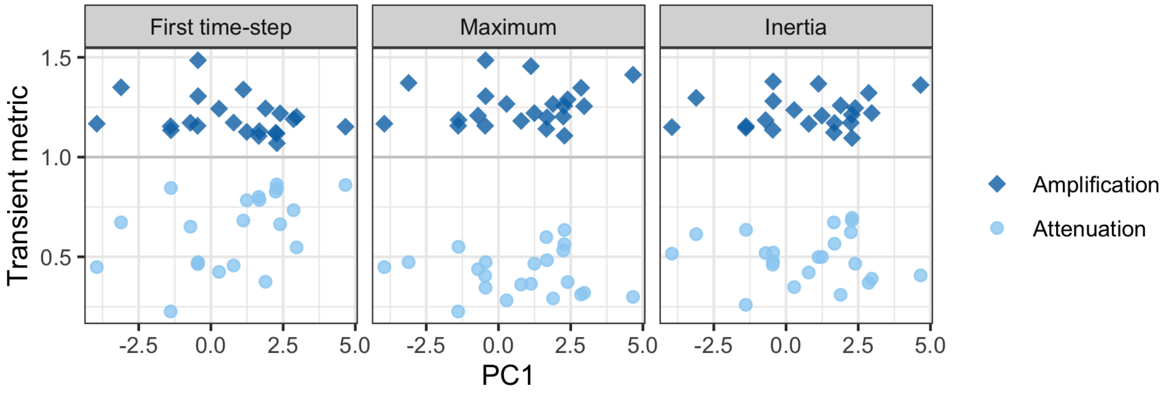

Figure 4.5: First time-step attenuation was associated with pace of life but other transient indices of short-term dynamics did not vary with pace of life.

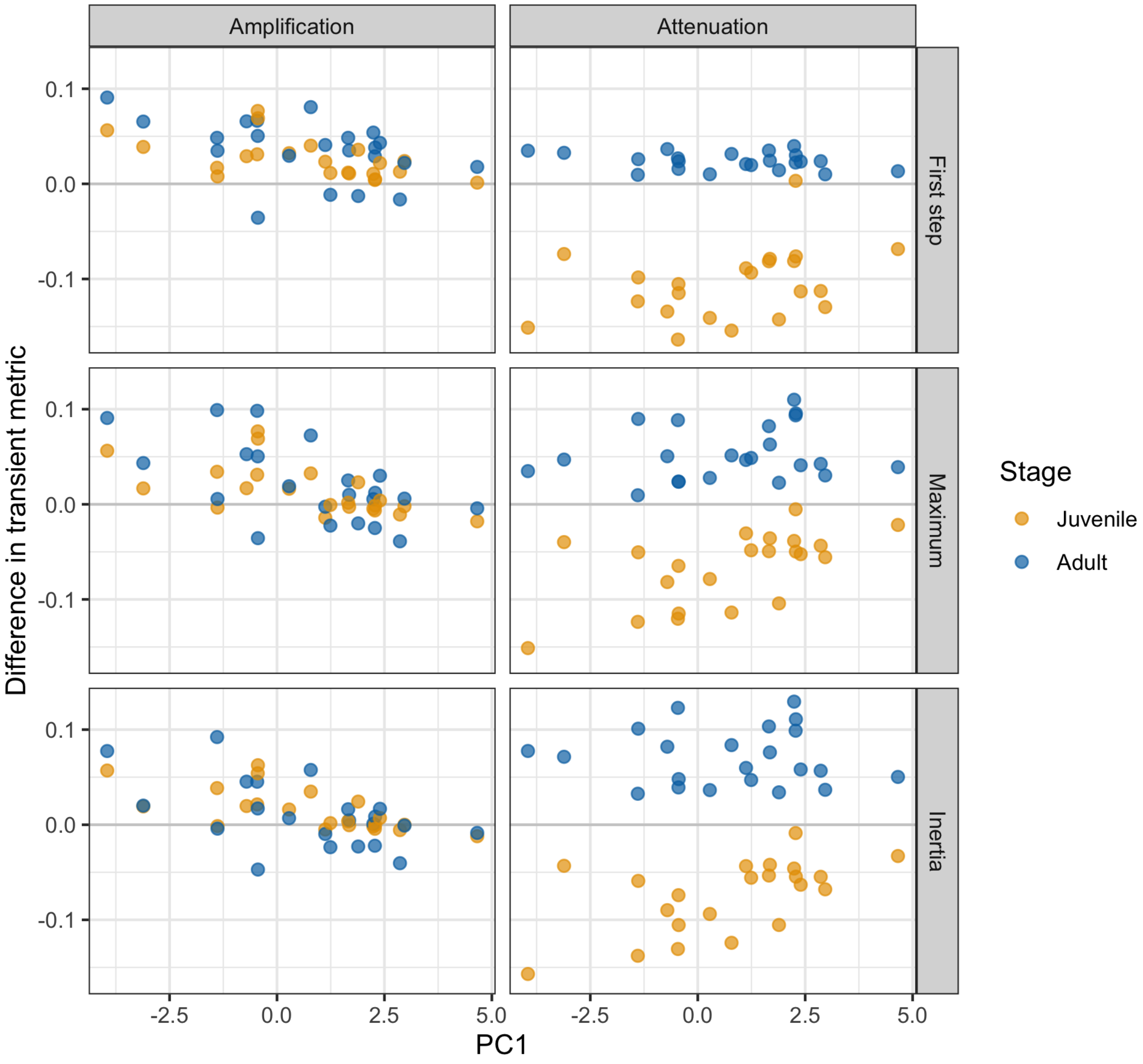

Figure 4.6: Sensitivity of short-term amplification metrics to perturbations of mortality hazard rate was negatively related to pace of life. Sensitivity of short-term attenuation metrics tended to be positively related with pace of life but intercepts, and slopes for attenuated inertia, differed for perturbations of juvenile and adult mortality hazard rate. Results are shown for increasing mortality hazard rate by 50%.

the exception of first time-step attenuation ($\underline{\rho}_1 = 0.6 + 0.04PC1$, $R^2 = 0.21$; $\underline{\rho}_1 = 0.42 + 0.02G$, $R^2 = 0.18$), transient metrics showed no relationship with pace of life (Fig. 4.5). Pace of life was related to changes in transients bounds produced by perturbations to stage-specific mortality hazard rate, with similar patterns among related metrics. Here, we present results for increasing mortality hazard rate by 50% (Fig. 4.6). For first time-step amplification, sensitivity to perturbations of mortality hazard rate was negatively related to pace of life. ($\Delta\bar{\rho}_{1juv} = 0.03 - 0.01PC1$, $\Delta\bar{\rho}_{1ad} = 0.04 - 0.01PC1$, $R^2 = 0.27$, slopes and intercepts not significantly different). Sensitivity of first-time step attenuation tended to be positively related with pace of life, but intercepts differed for perturbations of juvenile and adult mortality hazard rate ($\Delta\underline{\rho}_{1juv} = -0.11 + 0.01PC1$, $\Delta\underline{\rho}_{1ad} = 0.02 - 0.001PC1$, $R^2 = 0.87$, slopes not significantly different). Results for the other amplification and attenuation metrics and for generation length followed the same patterns, with slopes differing in some cases (e.g. for attenuated inertia, Fig. 4.6). Damping ratio showed a negative relationship with life history (Fig. 4.7), indicating a slower rate of recovery in slower maturing species. Both PC1 and generation length explained a significant amount of variation in damping ratio (PC1: $F = 17.55$, $d.f. = 1$, $p < 0.001$; generation length: $F = 13.73$, $d.f. = 1$, $p < 0.01$). Damping ratio was not significantly associated with adult body mass or population growth rate, λ.

4.4 Discussion

Understanding how species' demographic responses and resilience respond to elevated risks of mortality is necessary for effective conservation planning and prioritisation (Field et al. 2019, Capdevila et al. 2020). However, the analysis required to inform such prioritisation is often hindered by the scarcity of data on vital rates of mortality/survival, growth, and reproduction among species of conservation concern (González-Suárez et al. 2012, Roberts et al. 2016). Here, we use pace of life indicators that are more easily determined to assess risk to population growth of increased mortality. This approach compensates for the lack of hard to collect vital rates, potentially overcoming the issue of incomplete data and providing a novel means of assessing threats associated with increased mortality.

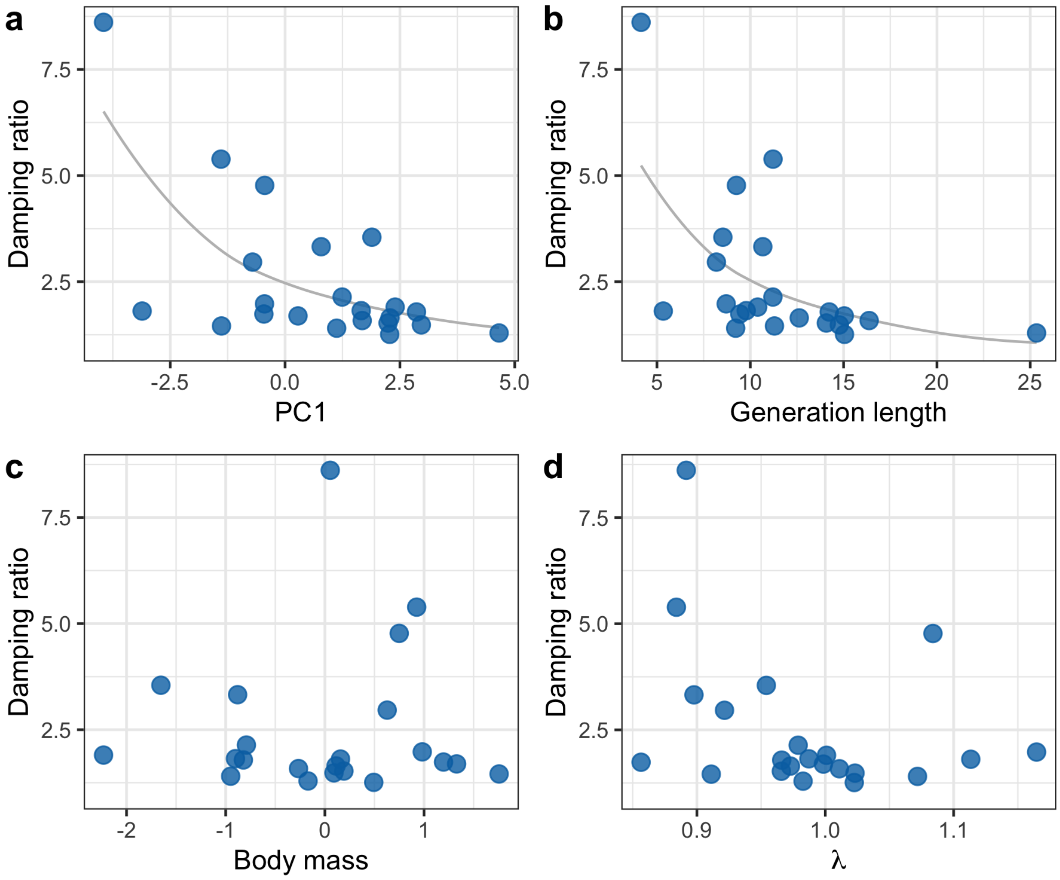

Figure 4.7: Damping ratio showed a negative relationship with life history proxies. Prediction lines indicate support for a relationship between damping ratio and the independent variable: a) PC1, b) generation length, c) body mass, and d) population growth rate, λ.

4.4.1 Classical sensitivity analysis

Sensitivity analysis is an important tool for conservation demography, allowing identification of lifecycle stages and vital rates with the greatest potential to mediate changes to population growth (Benton and Grant 1999). It is valuable when robust estimates of vital rates are available to parameterise demographic models (Beissinger and Westphal 1998, Coulson et al. 2001). We applied sensitivity and elasticity analysis of population growth rate to mortality hazard rate, averaged over an annual timestep, to predict the impact on population dynamics of mortality affecting juvenile or adult stages in seabirds. These baseline results support predictions from theory that, in slow-paced species, adult survival contributes most to asymptotic population growth rate (Heppell et al. 2000, Sæther and Bakke 2000, Oli and Dobson 2003). We found that, in seabirds, elasticity to adult mortality hazard rate was greater in magnitude than elasticity to juvenile mortality hazard rate. Among transient metrics, sensitivity to perturbations of juvenile and adult mortality rate differed between amplification and attenuation metrics. We found a similar magnitude of increase in amplification metrics in response to increased juvenile or adult mortality hazard rate. Attenuation metrics, in contrast, were higher when adult mortality hazard rate increased and lower in response to increased juvenile mortality hazard rate. These results reflect different influences of adult and juvenile life stages on short- and long-term population dynamics.

4.4.2 Relating sensitivity to pace of life using proxies

While classical sensitivity analysis is a valuable tool, parameterising the models used to derive sensitivity values requires detailed information about a species' lifecycle, such as stage-specific survival rates, which may be missing, particularly for species of conservation concern (González-Suárez et al. 2012, Conde et al. 2019). It would be valuable, therefore, to be able to predict sensitivity and elasticity using more readily available trait data to act as proxies for vital rates.

We explored the use of two proxies as predictors of sensitivity and elasticity: firstly, the major axis of a principal component analysis applied to representative life history traits (age at maturity, longevity, and clutch size), and secondly, generation length, which combines estimates of survival, age at maturation, and longevity. In addition, we considered two further predictors: body mass, which is known to covary with vital rates (Stearns 1983, Jeschke and

Kokko 2009), and asymptotic population growth rate, λ, since elasticities vary with population growth rate (de Kroon et al. 2000). Overall, we found some evidence that pace of life proxies were effective: they provide an indication of demographic responses to mortality in seabirds, particularly a relationship between mortality elasticities and transient sensitivities and pace of life, and a tendency for slower recovery in slow-lived species. However, we found some patterns in opposite directions than we expected. Here we discuss these outcomes.

We did not detect a relationship between the sensitivity of asymptotic population growth rate to mortality hazard rate and pace of life. However, we found that the magnitude of the elasticity of population growth rate to adult and juvenile mortality hazard rate tended to decrease for slower maturing species. This result is contrary to our expectation that elasticity to adult mortality hazard rate would be greatest in magnitude for species with the slowest pace of life (Sæther and Bakke 2000, Oli and Dobson 2003). The decrease in the proportional contribution of adult mortality rate to population growth rate with pace of life could reflect increases in the proportional contributions of mortality hazard rate for immature stages as the age of maturity increases (Heppell et al. 2000).

We found no relationship in seabirds between sensitivity and elasticity of population growth rate to mortality hazard rate and body mass. Heppell et al. (2000) noted that covariation between body size and traits such as age at maturation and litter sizes in mammals (Stearns 1983) produced differences in patterns of elasticity that could be linked to body size. The limited range of body mass for the species in our study (124 g *Sterna hirundo* to 4400 g *Gavia immer*) may be insufficient to detect such patterns, compared with a study like Heppell et al. (2000), which included mammals as diverse as small rodents and large cetaceans. Our results indicate that, within more restricted taxonomic groups, body size may serve as a poor proxy for the sensitivity of population growth rate to mortality hazard rate.

Sensitivity to mortality hazard rate tended to increase in magnitude with population growth rate, becoming more negative as λ increased, but elasticity did not show a relationship with λ. For slower paced species in our data set, λ tended to be close to 1; more extreme values of λ tended to be associated with lower values of PC1 (Fig. S4.1) and with more negative elasticities (Fig. 4.4d). These interrelationships between pace of life, population growth rate and elasticity to mortality hazard rate suggest that, although we detected a relationship between pace of life and elasticity to mortality hazard rate that appears to be quite robust, our results may be linked to covariation between pace of life and population growth rate in our data set. While our results tentatively support the use of pace of life proxies to determine elasticity to adult and juvenile mortality hazard rate in seabirds, further work would be valuable to determine whether the pattern is independent of population growth rate. Our results suggest that the proportional impact of mortality on first year juvenile and adult stages decreases as pace of life slows, perhaps reflecting the growing importance of immature stages as age at maturity increases. Efforts to understand impacts on immature stages may be increasingly important for slower paced species.

4.4.3 Transient dynamics and pace of life proxies

In our analysis of seabirds, pace of life was not a useful proxy for metrics describing the bounds on transient dynamics. However, the sensitivity of transient metrics to mortality hazard rate was related to pace of life, with sensitivity to amplification and attenuation metrics tending to decrease in magnitude with pace of life. The lack of association between pace of life and transient metrics contrasts with results for mammals that link transient dynamics to life history, with slow-paced species more likely to display a reduction in population density in response to disturbance (Gamelon et al. 2014). Although we included species spanning a range of life histories at the slower end of the life history spectrum, the variety of life history in our study is limited compared to that of Gamelon et al. (2014), which encompassed 111 species with generation time spanning two orders of magnitude (2.6 years *Cynomys gunnisoni* to 102.9 years *Rhinoceros unicornis*). In that study, transient metrics were combined using phylogenetic PCA, producing major axes of variation that captured attenuation and amplification metrics respectively. Similarity among amplification and attenuation metrics (Fig. 4.5) in our study suggest that we would find similar alignments among transient metrics. Detection of a relationship between life history and transient metrics may require a broader comparative scope than in our study. For example, in a study of plants ranging from monocarpic plants to trees, species at either end of the fast-slow continuum showed the greatest potential for transient amplification and attenuation (Stott et al. 2010).

Our results suggest a relatively limited potential in seabirds for an increase in population size following perturbation to population structure, with amplification metrics indicating a maximum of around 25% increase in population size. There appears to be greater potential for populations to decrease in size following perturbation, with maximum and long-term attenuation of around 50% and fairly high among-species variation. Perturbation of mortality hazard rate caused changes to transient bounds which were weakly related to pace of life, with greater changes tending to occur in faster paced species. Understanding the drivers for differences in attenuation among species is important for understanding the potential for populations to be negatively impacted in response to threats. Our study suggests that pace of life has limited use as a surrogate in this case, and that alternative indicators such as ecological traits should be considered.

Although pace of life was not a strong indicator of transient amplification and attenuation, we found evidence to suggest that pace of life can predict recovery time following perturbation, captured here by the damping ratio. Our results suggest that, as pace of life slows, populations become slower to return to a stable population state. Slow recovery in longer-lived species can increase their vulnerability to threats such as habitat loss, harvest or natural catastrophes (Keevil et al. 2018, Capdevila et al. 2020). The ability to predict which populations will take longer to recover from impacts could be used in impact assessments and to target mitigation efforts towards the most vulnerable populations.

4.4.4 Limitations

We considered the impact of increased mortality hazard rate for single lifecycle stages. However, threats could affect vital rates across the lifecycle simultaneously and interactions between stage-specific perturbations may amplify impacts on population dynamics (Hunter and Caswell 2005). Furthermore, threats that affect a given vital rate may have an opposing influence on another rate (Barbraud and Weimerskirch 2001). Sensitivities of population growth rate to perturbations of vital rates for multiple lifecycle stages could be calculated through application of the chain rule (Jenouvrier et al. 2018) to explore synergistic responses. However, interpreting the results in terms of pace of life indicators would be more complicated.

As well as affecting multiple vital rates, threats may affect different parts of the lifecycle according to spatial and temporal patterns of behaviour. Failure to account for impacts across the lifecycle may lead to biased assessment of risk (Carneiro et al. 2020). Here, adopting a stage-based approach allowed us to explore the impact of mortality occurring at different lifecycle stages. To assess the impact of increased mortality affecting only part of the annual lifecycle one would need to use a model with a seasonal time step. We would not expect the results of a seasonal model to differ greatly from our results based on mortality hazard rate averaged across the annual time step.

Our focus on a single vital rate, time-averaged mortality hazard rate, derived from the probability of survival over the annual time step, reflects the importance of survival in the lifecycle of long-lived species. Mortality hazard rate has the advantage of being on a non-bounded scale, allowing the calculation of sensitivities and elasticities on a scale that is readily comparable with sensitivities to other vital rates (Ergon et al. 2018). While adult survival is the vital rate with the greatest proportional effect on population growth rate in slow-paced species, other vital rates may also contribute to both long-term and transient population dynamics.

4.4.5 Implications for management of vulnerable seabirds

Despite the ability of many species to buffer environmental change through behavioural plasticity (Grémillet et al. 2012, Field et al. 2019), seabirds remain at risk from a wide range of threats. Environmental contaminants such as oil spills and marine plastics can cause direct mortality (Votier et al. 2005) or contribute to reduced body condition and result in negative effects on survival and recruitment (Lavers et al. 2014). Incidental bycatch leads to increased mortality in albatrosses, petrels and shearwaters (Anderson et al. 2011, Paterson et al. 2019) and may be particularly associated with immature mortality (Barbraud et al. 2012). Overfishing is associated with reduced breeding success (Wanless et al. 2007, Carroll et al. 2017) and with low adult body condition (Grémillet et al. 2016), which may affect breeding success and adult survival. Other threats may affect survival (e.g. artificial lighting, Rodríguez et al. 2017) or reproductive success (e.g. disturbance, Watson et al. 2014; invasive species, Spatz et al. 2017). Combined threats may produce complex effects on vital rates, for example when negative effects on survival and breeding success due to changes in climatic conditions interact with the negative impact of fisheries on survival (Rolland et al. 2010, Barbraud et al. 2012). Demographic metrics provide a common currency to quantify and compare the potential population-level consequences of these impacts.

Previous work has indicated that life history traits can modulate seabird species' responses to threats (Sandvik et al. 2012, Genovart et al. 2013). As noted above, we found that pace of life proxies based on life history traits can provide an indication of demographic responses to mortality in seabirds, particularly relationships between mortality elasticities and pace of life and between transient sensitivities and pace of life, and a tendency for slower recovery in slow-paced species. For seabirds, use of pace of life proxies as indicators of elasticity to mortality hazard rate and the sensitivity of transient fluctuations could be important when assessing the impact of threats which are expected to increase mortality but for which direct evidence for mortality impacts is lacking, such as offshore developments (Burke et al. 2012). A similar approach could be used to assess population responses to impacts on reproductive success, with the indicators combined to provide an overall assessment of vulnerability. Damping ratio provides a useful metric of the time needed to recover from perturbations such as severe weather events (Jenouvrier et al. 2009) or mortality induced by human activities such as oil spills (Votier et al. 2005). Many seabird populations face multiple or repeated threats (Dias et al. 2019), and for species with low damping ratio the potential for recovery could be seriously hindered.

Our results suggest that pace of life indicators such as generation length could be used as a means of assessing threat in seabirds. The utility of generation length as a natural time scale for assessing population dynamics is widely recognised (Frankham and Brook 2004, Sæther et al. 2005, O'Grady et al. 2008) and has shaped its use in conservation biology. In particular, generation length is used to adjust the period over which to assess population trends in the International Union for Conservation of Nature (IUCN) Red List assessment, allowing this time scale to account for differences in life history among species (Mace et al. 2008, IUCN Standards and Petitions Subcommittee 2019). Substantial effort has consequently been applied to produce robust generation length estimates in many taxa (e.g. mammals, Pacifici et al. 2013, Cooke et al. 2018; birds, Bird et al. 2020). Such estimates could be used to rank seabird species of conservation concern, providing a potential shortcut to assessing species' vulnerability to threats that affect vital rates such as mortality hazard rate. Furthermore, pace of life indicators could be combined with ecological and behavioural indicators (Furness et al. 2013, Kelsey et al. 2018) to provide a more comprehensive indication of species' responses to threats. Reliable indicators are necessary to provide robust assessment of risks to marine birds from threats such as human activities and extreme climatic events so that appropriate mitigation can be planned and implemented.

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4.6 Author contributions

T.D.J., D.Z.C. and A.P.B. conceived and designed the study. T.D.J. performed data collection, carried out the analysis and wrote the manuscript. D.Z.C. and A.P.B. contributed critically to the drafts and gave final approval for publication.

4.7 References

Anderson ORJ, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O, Black A. 2011. Global seabird bycatch in longline fisheries. *Endangered Species Research*, **14**(2), 91–106.

Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H. 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Marine Ecology Progress Series*, **454**, 285–307.

Barbraud C, Weimerskirch H. 2001. Emperor penguins and climate change. *Nature*, **411**(6834), 183–186.

Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability in endangered species management. *The Journal of Wildlife Management*, **62**(3), 821–841.

Benton TG, Grant A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology & Evolution*, **14**(12), 467–471.

Bienvenu F, Legendre S. 2015. A new approach to the generation time in matrix population models. *The American Naturalist*, **185**(6), 834–843.

Bird JP, Martin R, Akçakaya HR, Gilroy J, Burfield IJ, Garnett ST, Symes A, Taylor J, Şekercioğlu ÇH, Butchart SHM. 2020. Generation lengths of the world's birds and their implications for extinction risk. *Conservation Biology*, **34**(5), 1252–1261.

Burke CM, Montevecchi WA, Wiese FK. 2012. Inadequate environmental monitoring around offshore oil and gas platforms on the Grand Bank of Eastern Canada: Are risks to marine birds known? *Journal of Environmental Management*, **104**, 121–126.

Capdevila P, Stott I, Beger M, Salguero-Gómez R. 2020. Towards a comparative framework of demographic resilience. *Trends in Ecology & Evolution*, **35**(9), 776–786.

Carneiro APB, et al. 2020. A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology. *Journal of Applied Ecology*, **57**(3), 514–525.

Carroll MJ, Bolton M, Owen E, Anderson GQA, Mackley EK, Dunn EK, Furness RW. 2017. Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **27**(6), 1164–1175.

Carslake D, Townley S, Hodgson DJ. 2009. Predicting the impact of stage-specific harvesting on population dynamics. *Journal of Animal Ecology*, **78**(5), 1076–1085.

Caswell H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Mass., 2nd ed.

Conde DA, et al. 2019. Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences*, **116**(19), 9658–9664.

Cooke RSC, Gilbert TC, Riordan P, Mallon D. 2018. Improving generation length estimates for the IUCN Red List. *PLOS ONE*, **13**(1), e0191770.

Coulson T, Mace GM, Hudson E, Possingham H. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution*, **16**(5), 219–221.

de Kroon H, van Groenendael J, Ehrlén J. 2000. Elasticities: a review of methods and model limitations. *Ecology*, **81**(3), 607–618.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Croxall JP. 2019. Threats to seabirds: a global assessment. *Biological Conservation*, **237**, 525–537.

Ergon T, Borgan Ø, Nater CR, Vindenes Y. 2018. The utility of mortality hazard rates in population analyses. *Methods in Ecology and Evolution*, **9**(10), 2046–2056.

Ezard THG, Bullock JM, Dalgleish HJ, Millon A, Pelletier F, Ozgul A, Koons DN. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology*, **47**(3), 515–523.

Field CR, Ruskin KJ, Cohen JB, Hodgman TP, Kovach AI, Olsen BJ, Shriver WG, Elphick CS. 2019. Framework for quantifying population responses to disturbance reveals that coastal birds are highly resilient to hurricanes. *Ecology Letters*, **22**(12), 2039–2048.

Frankham R, Brook BW. 2004. The importance of time scale in conservation biology and ecology. *Annales Zoologici Fennici*, **41**(3), 459–463.

Furness RW, Tasker ML. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, **202**, 253–264.

Furness RW, Wade HM, Masden EA. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, **119**, 56–66.

Gaillard JM, Yoccoz NG, Lebreton JD, Bonenfant C, Devillard S, Loison A, Pontier D, Allaine D. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. *The American Naturalist*, **166**(1), 119–123.

Gamelon M, Gimenez O, Baubet E, Coulson T, Tuljapurkar S, Gaillard JM. 2014. Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. *The American Naturalist*, **184**(5), 673–683.

Garthe S, Hüppop O. 2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology*, **41**(4), 724–734.

Genovart M, Sanz-Aguilar A, Fernández-Chacón A, Igual JM, Pradel R, Forero MG, Oro D. 2013. Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. *Journal of Animal Ecology*, **82**(1), 121–130.

González-Suárez M, Lucas PM, Revilla E. 2012. Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology*, **81**(6), 1211–1222.

Grémillet D, Charmantier A. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecological Applications*, **20**(6), 1498–1503.

Grémillet D, Péron C, Kato A, Amélineau F, Ropert-Coudert Y, Ryan PG, Pichegru L. 2016. Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem. *Marine Biology*, **163**(2), 35.

Grémillet D, Welcker J, Karnovsky NJ, Walkusz W, Hall ME, Fort J, Brown ZW, Speakman JR, Harding AMA. 2012. Little auks buffer the impact of current Arctic climate change. *Marine Ecology Progress Series*, **454**, 197–206.

Hastings A. 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology & Evolution*, **19**(1), 39–45.

Heppell SS, Caswell H, Crowder LB. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, **81**(3), 654–665.

Horswill C, Robinson R. 2015. Review of Seabird Demographic Rates and Density Dependence. JNCC Report 552, Joint Nature Conservation Committee.

Hunter CM, Caswell H. 2005. Selective harvest of sooty shearwater chicks: effects on population dynamics and sustainability. *Journal of Animal Ecology*, **74**(4), 589–600.

IUCN Standards and Petitions Subcommittee. 2019. Guidelines for using the IUCN Red List categories and criteria. Tech. Rep. Version 14, prepared by the Standards and Petitions Subcommittee. Available from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed November 2019).

Jenouvrier S, Barbraud C, Weimerskirch H. 2005. Long-term contrasted responses to climate of two antarctic seabird species. *Ecology*, **86**(11), 2889–2903.

Jenouvrier S, Caswell H, Barbraud C, Holland M, Stroeve J, Weimerskirch H. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences*, **106**(6), 1844–1847.

Jenouvrier S, Desprez M, Fay R, Barbraud C, Weimerskirch H, Delord K, Caswell H. 2018. Climate change and functional traits affect population dynamics of a long-lived seabird. *Journal of Animal Ecology*, **87**(4), 906–920.

Jeschke JM, Kokko H. 2009. The roles of body size and phylogeny in fast and slow life histories. *Evolutionary Ecology*, **23**(6), 867–878.

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR. 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology*, **22**(1), 16–26.

Keevil MG, Brooks RJ, Litzgus JD. 2018. Post-catastrophe patterns of abundance and survival reveal no evidence of population recovery in a long-lived animal. *Ecosphere*, **9**(9), e02396.

Kelsey EC, Felis JJ, Czapanskiy M, Pereksta DM, Adams J. 2018. Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. *Journal of Environmental Management*, **227**, 229–247.

Koons DN, Grand JB, Zinner B, Rockwell RF. 2005. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, **185**(2), 283–297.

Lavers JL, Bond AL, Hutton I. 2014. Plastic ingestion by Flesh-footed Shearwaters (Puffinus carneipes): Implications for fledgling body condition and the accumulation of plastic-derived chemicals. *Environmental Pollution*, **187**, 124–129.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland E, Stuart SN. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**(6), 1424–1442.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, **96**(11), 3109–3109.

O'Grady JJ, Reed DH, Brook BW, Frankham R. 2008. Extinction risk scales better to generations than to years. *Animal Conservation*, **11**(5), 442–451.

Oli MK, Dobson FS. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *The American Naturalist*, **161**(3), 422–440.

Pacifici M, Santini L, Marco MD, Baisero D, Francucci L, Marasini GG, Visconti P, Rondinini C. 2013. Generation length for mammals. *Nature Conservation*, **5**, 89–94.

Paterson JRB, Yates O, Holtzhausen H, Reid T, Shimooshili K, Yates S, Sullivan BJ, Wanless RM. 2019. Seabird mortality in the Namibian demersal longline fishery and recommendations for best practice mitigation measures. *Oryx*, **53**(2), 300–309.

Péron G, et al. 2016. Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution*, **70**(12), 2909–2914.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramula S, Knight TM, Burns JH, Buckley YM. 2008. General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology*, **45**(4), 1124–1133.

Read AF, Harvey PH. 1989. Life history differences among the eutherian radiations. *Journal of Zoology*, **219**(2), 329–353.

Revell LJ. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution*, **63**(12), 3258–3268.

Roberts BEI, Harris WE, Hilton GM, Marsden SJ. 2016. Taxonomic and geographic bias in conservation biology research: a systematic review of wildfowl demography studies. *PLOS ONE*, **11**(5), e0153908.

Rodríguez A, et al. 2017. Seabird mortality induced by land-based artificial lights. *Conservation Biology*, **31**(5), 986–1001.

Rolland V, Weimerskirch H, Barbraud C. 2010. Relative influence of fisheries and climate on the demography of four albatross species. *Global Change Biology*, **16**(7), 1910–1922.

Sæther BE, Bakke Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**(3), 642–653.

Sæther BE, et al. 2005. Generation time and temporal scaling of bird population dynamics. *Nature*, **436**(7047), 99–102.

Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, Kroon Hd, Buckley YM. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, **113**(1), 230–235.

Sandvik H, Erikstad KE, Sæther BE. 2012. Climate affects seabird population dynamics both via reproduction and adult survival. *Marine Ecology Progress Series*, **454**, 273–284.

Spatz DR, Holmes ND, Reguero BG, Butchart SHM, Tershy BR, Croll DA. 2017. Managing invasive mammals to conserve globally threatened seabirds in a changing climate. *Conservation Letters*, **10**(6), 736–747.

Stahl JT, Oli MK. 2006. Relative importance of avian life-history variables to population growth rate. *Ecological Modelling*, **198**(1–2), 23–39.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**(2), 173–187.

Stott I, Franco M, Carslake D, Townley S, Hodgson D. 2010. Boom or bust? A comparative analysis of transient population dynamics in plants. *Journal of Ecology*, **98**(2), 302–311.

Stott I, Hodgson DJ, Townley S. 2012. Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. *Methods in Ecology and Evolution*, **3**(4), 673–684.

Stott I, Townley S, Hodgson DJ. 2011. A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, **14**(9), 959–970.

Tacutu R, et al. 2018. Human Ageing Genomic Resources: new and updated databases. *Nucleic Acids Research*, **46**(D1), D1083–D1090.

Votier SC, Hatchwell BJ, Beckerman A, McCleery RH, Hunter FM, Pellatt J, Trinder M, Birkhead TR. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters*, **8**(11), 1157–1164.

Wanless S, Frederiksen M, Daunt F, Scott BE, Harris MP. 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Progress in Oceanography*, **72**(1), 30–38.

Watson H, Bolton M, Monaghan P. 2014. Out of sight but not out of harm's way: human disturbance reduces reproductive success of a cavity-nesting seabird. *Biological Conservation*, **174**, 127–133.

4.8 Supporting information

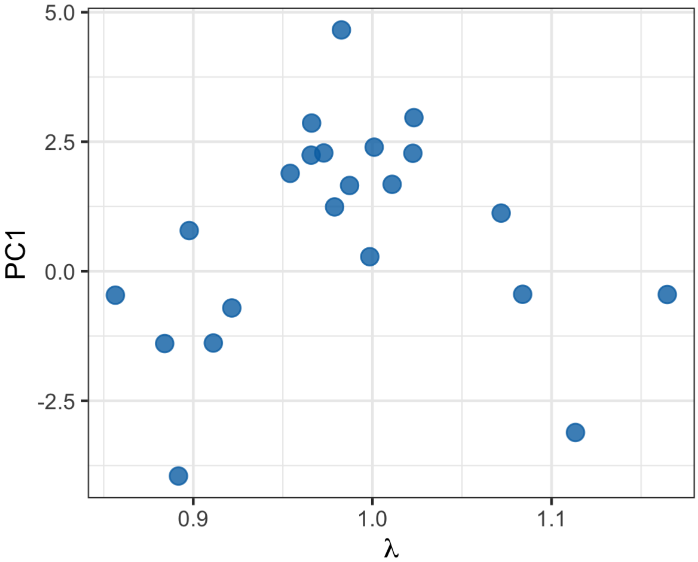

Figure S4.1: Relationship between asymptotic population growth rate λ and life history indicator, PC1.

Table S4.1: Demographic data for species included in the analysis. References indicate original sources for the demographic data from Horswill and Robinson (2015).

Scientific name	Common name	Demographic parameter	Mean	SD_p	SE_e	References
Alca torda	Razorbill	Immature survival, 0-2 years (composite)	0.63	0.209		Lavers et al 2008
Alca torda	Razorbill	Adult survival, $\geq$3 year	0.895	0.067		Taylor et al 2010, Lahoz-Monfort et al 2011
Alca torda	Razorbill	Productivity	0.57	0.247		Mavor et al 2008, Lloyd 1979, Newell et al 2010, Shaw et al 2010
Alca torda	Razorbill	Age of recruitment	5			
Alca torda	Razorbill	Missed breeding	0.03			Harris & Wanless 1989
Aythya marila	Greater scaup	Juvenile survival, 0-1 year	0.4			Flint et al 2006
Aythya marila	Greater scaup	Adult survival	0.81		0.038	Flint et al 2006
Aythya marila	Greater scaup	Productivity	0.57		0.12	Flint et al 2006
Aythya marila	Greater scaup	Age of recruitment	2			Dementiev & Gladkov 1952
Cepphus grylle	Black guillemot	Juvenile survival, 0-1 year	0.731	0.239		Frederiksen & Petersen 1999a
Cepphus grylle	Black guillemot	Adult survival	0.87	0.034		Frederiksen & Petersen 1999a
Cepphus grylle	Black guillemot	Productivity	1.298	0.315		Mavor et al 2008
Cepphus grylle	Black guillemot	Age of recruitment	5			Frederiksen 1998
Fratercula arctica	Atlantic puffin	Immature survival, 0-3 years	0.709		0.022	Breton et al 2006
Fratercula arctica	Atlantic puffin	Immature survival, 3-4 years	0.76		0.019	Breton et al 2006
Fratercula arctica	Atlantic puffin	Immature survival, 4-5 years	0.805		0.017	Breton et al 2006
Fratercula arctica	Atlantic puffin	Adult survival, $\geq$6 year	0.906	0.083		Harris et al 2005, Lahoz-Monfort et al 2011, Taylor et al 2010
Fratercula arctica	Atlantic puffin	Productivity	0.617	0.151		Taylor et al 2010, Shaw et al 2010, Mavor et al 2008, Newell et al 2010, Ashcroft 1979, Harris 1980
Fratercula arctica	Atlantic puffin	Age of recruitment	5			Ashcroft 1979, Harris 1983
Fratercula arctica	Atlantic puffin	Missed breeding	0.078			Ashcroft 1979
Fulmarus glacialis	Northern fulmar	Immature survival, 0-8 years (composite)	0.26	0.15		Jenouvrier et al 2003
Fulmarus glacialis	Northern fulmar	Adult survival	0.936	0.055		Grosbois & Thompson 2005
Fulmarus glacialis	Northern fulmar	Productivity	0.419	0.127		Mavor et al 2008, Shaw et al 2010, Lewis et al 2009, Newell et al 2010, Büche et al 2013
Fulmarus glacialis	Northern fulmar	Age of recruitment	9			Ollason & Dunnet 1978b
Gavia arctica	Black-throated diver	Juvenile survival, 0-1 year	0.4			Hemmingsson & Eriksson 2002

Gavia arctica	Black-throated diver	Adult survival, ≥2 year	0.817	0.064		Hemmingsson & Eriksson 2002, Nilsson 1977
Gavia arctica	Black-throated diver	Productivity	0.425	0.292		Mudge & Talbot 1993, Hancock 2000, Sharrock 1976, Jackson 2003, Bundy 1979, Thom 1986
Gavia arctica	Black-throated diver	Age of recruitment	5			Lehtonen 1970
Gavia immer	Great northern diver	Immature survival, 0-3 year	0.77		0.02	Piper et al 2012
Gavia immer	Great northern diver	Adult survival, ≥4 year	0.87		0.078	Piper et al 2012, Mitro et al 2008
Gavia immer	Great northern diver	Productivity	0.543	0.17		Belant & Anderson 1991, Croskery 1991, Timmermans et al 2005, Grear et al 2009
Gavia immer	Great northern diver	Age of recruitment	6			Evers 2004
Gavia immer	Great northern diver	Missed breeding	0.307			Evers 2004
Gavia stellata	Red-throated diver	Juvenile survival, 0-1 year	0.6			Hemmingsson & Eriksson 2002
Gavia stellata	Red-throated diver	Immature survival, 1-2 year	0.62			Hemmingsson & Eriksson 2002
Gavia stellata	Red-throated diver	Adult survival, ≥3 year	0.84		0.074	Hemmingsson & Eriksson 2002, Schmutz 2014
Gavia stellata	Red-throated diver	Productivity	0.571	0.222		Gomersall 1986, Booth 1999
Gavia stellata	Red-throated diver	Age of recruitment	3			Okill 1994
Larus argentatus	Herring gull	Juvenile survival, 0-1 year	0.798	0.092		Chabrzyk & Coulson 1976, Harris 1970
Larus argentatus	Herring gull	Adult survival, ≥2 year	0.834	0.034		Wanless et al 1996, Taylor et al 2010
Larus argentatus	Herring gull	Productivity	0.92	0.477		Mavor et al 2008, Kim & Monaghan 2005a, Swann 2010
Larus argentatus	Herring gull	Age of recruitment	5			Harris 1970
Larus argentatus	Herring gull	Missed breeding	0.35	0.028		Calladine & Harris 1997
Larus canus	Common or mew gull	Juvenile survival, 0-1 year	0.41			Rattiste & Lilleleht 1987
Larus canus	Common or mew gull	Immature survival, 1-2 years	0.71			Rattiste & Lilleleht 1987
Larus canus	Common or mew gull	Adult survival, ≥3 year	0.828	0.05		Rattiste 2004
Larus canus	Common or mew gull	Productivity	0.543	0.391		Mavor et al 2008, Shaw et al 2010
Larus canus	Common or mew gull	Age of recruitment	3			Rattiste & Lilleleht 1987
Larus fuscus	Lesser black-backed gull	Juvenile survival, 0-1 year	0.82			Harris 1970
Larus fuscus	Lesser black-backed gull	Adult survival, >2 year	0.885	0.022		Wanless et al 1996, Taylor et al 2010
Larus fuscus	Lesser black-backed gull	Productivity	0.53	0.325		Mavor et al 2008
Larus fuscus	Lesser black-backed gull	Age of recruitment	5			Harris 1970
Larus fuscus	Lesser black-backed gull	Missed breeding	0.337	0.065		O'Connell et al 1997,
Melanitta nigra	Common scoter	Juvenile survival, 0-1 year	0.749		0.056	Fox et al 2003
Melanitta nigra	Common scoter	Adult survival	0.783		0.032	Fox et al 2003
Melanitta nigra	Common scoter	Productivity	1.838	1.184		Gardarsson and Einarsson 2004
Melanitta nigra	Common scoter	Age of recruitment	3			Bengtson 1972
Morus bassanus	Northern gannet	Juvenile survival, 0-1 year	0.424		0.007	Wanless et al 2006

Morus bassanus	Northern gannet	Immature survival, 1-2 years	0.829		0.004	Wanless et al 2006
Morus bassanus	Northern gannet	Immature survival, 2-3 years	0.891		0.003	Wanless et al 2006
Morus bassanus	Northern gannet	Immature survival, 3-4 years	0.895		0.003	Wanless et al 2006
Morus bassanus	Northern gannet	Adult survival, $\geq$ 5 years	0.919	0.042		Wanless et al 2006
Morus bassanus	Northern gannet	Productivity	0.7	0.082		Wanless et al 2006, Nelson 1966, Mavor et al 2008, Shaw 2010
Morus bassanus	Northern gannet	Age of recruitment	5			Wanless et al 2006, Nelson 1966
Phalacrocorax aristotelis	European shag	Juvenile survival, 0-1 year	0.513	0.246		Frederiksen et al 2008
Phalacrocorax aristotelis	European shag	Immature survival, 1-2 year	0.737	0.181		Frederiksen et al 2008
Phalacrocorax aristotelis	European shag	Adult survival, $\geq$3 year	0.858	0.194		Frederiksen et al 2008
Phalacrocorax aristotelis	European shag	Productivity	1.303	0.483		Mavor et al 2008, Newell et al 2010
Phalacrocorax aristotelis	European shag	Age of recruitment	2			Aebischer 1986
Phalacrocorax carbo	Great cormorant	Juvenile survival, 0-1 year	0.54		0.09	Frederiksen & Bregnballe 2000a, Hénaux et al 2007
Phalacrocorax carbo	Great cormorant	Adult survival, >3 year	0.868	0.055		Frederiksen & Bregnballe 2000a, Hénaux et al 2007
Phalacrocorax carbo	Great cormorant	Productivity	1.985	0.666		Mavor et al 2008, Budworth et al 2000
Phalacrocorax carbo	Great cormorant	Age of recruitment	3			Kortlandt 1942, Frederiksen & Bregnballe 2000b
Rissa tridactyla	Black-legged kittiwake	Juvenile survival, 0-1 year	0.79			Coulson & White 1959
Rissa tridactyla	Black-legged kittiwake	Adult survival, $\geq$2 year	0.854	0.051		Frederiksen et al 2004a, , Taylor et al 2010
Rissa tridactyla	Black-legged kittiwake	Productivity	0.69	0.296		Mavor et al 2008, Shaw et al 2010, Newell et al 2010
Rissa tridactyla	Black-legged kittiwake	Age of recruitment	4			Wooller & Coulson 1977, Porter & Coulson 1987
Rissa tridactyla	Black-legged kittiwake	Missed breeding, increasing population	0.18	0.188		Danchin & Monnat 1992
Rissa tridactyla	Black-legged kittiwake	Missed breeding, decreasing population	0.208	0.207		Danchin & Monnat 1992
Somateria mollissima	Common eider	Juvenile survival, 0-1 year	0.2			Sperduto et al 2003
Somateria mollissima	Common eider	Adult survival, $\geq$2 year	0.886	0.009		Coulson 1984, Hario et al 2009
Somateria mollissima	Common eider	Productivity	0.379	0.47		Sweenen 1991, Hario & Rintala 2006, Lehikoinen et al 2006
Somateria mollissima	Common eider	Age of recruitment	3			Sperduto et al 2003, Christensen 1999
Somateria mollissima	Common eider	Missed breeding	0.2	0.141		Coulson 1984
Stercorarius parasiticus	Arctic skua	Immature survival, 0-4 years (composite)	0.346			O'Donald 1983
Stercorarius parasiticus	Arctic skua	Adult survival	0.91			Phillips & Furness 1998
Stercorarius parasiticus	Arctic skua	Productivity	0.487	0.436		Mavor et al 2008

Stercorarius parasiticus	Arctic skua	Age of recruitment	4			O'Donald & Davis 1975
Stercorarius parasiticus	Arctic skua	Missed breeding	0.03			Catry et al 1998
Stercorarius skua	Great skua	Immature survival, 0-5 years (composite)	0.73			Ratcliffe et al 2002
Stercorarius skua	Great skua	Adult survival	0.882	0.038		Ratcliffe et al 2002, Votier et al 2004
Stercorarius skua	Great skua	Productivity	0.651	0.308		Mavor et al 2008
Stercorarius skua	Great skua	Age of recruitment	7			Furness 1987
Stercorarius skua	Great skua	Missed breeding	0.089	0.04		Catry et al 1998
Sterna hirundo	Common tern	Immature survival, 0-2 years (composite)	0.441		0.004	Braasch et al 2008
Sterna hirundo	Common tern	Immature survival, 3-4 years	0.85			Breton et al 2014
Sterna hirundo	Common tern	Adult survival, >6 year	0.883	0.014		Breton et al 2014, Nisbet & Cam 2002
Sterna hirundo	Common tern	Productivity	0.764	0.47		Mavor et al 2008
Sterna hirundo	Common tern	Age of recruitment, min	3			Nisbet 1978, Ludwigs & Becker 2002a
Sterna hirundo	Common tern	Age of recruitment, max	4			Nisbet 1978, Ludwigs & Becker 2002a
Sterna sandvicensis	Sandwich tern	Juvenile survival, 0-1 year	0.358		0.219	Robinson 2010
Sterna sandvicensis	Sandwich tern	Immature survival, 2-3-4 years	0.741		0.206	Robinson 2010
Sterna sandvicensis	Sandwich tern	Adult survival	0.898		0.029	Robinson 2010
Sterna sandvicensis	Sandwich tern	Productivity	0.702	0.372		Mavor et al 2008
Sterna sandvicensis	Sandwich tern	Age of recruitment	3			Veen 1977
Uria aalge	Common guillemot	Juvenile survival, 0-1 year	0.56		0.013	Harris et al 2007
Uria aalge	Common guillemot	Immature survival, 1-2 year	0.792		0.034	Harris et al 2007
Uria aalge	Common guillemot	Immature survival, 2-3 year	0.917		0.022	Harris et al 2007
Uria aalge	Common guillemot	Adult survival, $\geq$4th year	0.939	0.015		Lahoz-Monfort et al 2011, Reynolds et al 2011, Meade et al 2013
Uria aalge	Common guillemot	Productivity	0.672	0.147		Meade et al 2013, Mavor et al 2008, Shaw et al 2010, Newell et al 2010
Uria aalge	Common guillemot	Age of recruitment	6			Halley & Harris 1993
Uria aalge	Common guillemot	Missed breeding	0.079			Harris & Wanless 1995

Chapter 5

Global analysis reveals complex demographic responses of mammals to climate change

Maria Paniw, Tamora D. James, C. Ruth Archer, Gesa Römer, Sam Levin, Aldo Compagnoni, Judy Che-Castaldo, Joanne M. Bennett, Andrew Mooney, Dylan Z. Childs, Arpat Ozgul, Owen R. Jones, Jean H. Burns, Andrew P. Beckerman, Abir Patwary, Nora Sanchez-Gassen, Tiffany M. Knight§, & Roberto Salguero-Gómez§

§Shared senior co-authorship

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5.1 Author contributions

M.P., T.D.J., G.R., and R.S.-G. devised the overall manuscript. M.P. and T.D.J. designed the literature review protocol, which was then implemented by M.P., T.D.J., G.R., C.R.A., S.L., A.M., J.C., N.S.G., J.M.B., and A.P. The climatic data were derived by A.C. The first draft of the manuscript was written by M.P. and R.S.-G., and all co-authors contributed to the final manuscript. See Section 5.3 for further specifics regarding task contributions.

5.2 Manuscript

Global analysis reveals complex demographic responses of mammals to climate change

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Keywords

Climate vulnerability; full life-cycle analyses; temperature extremes.

Abstract

Approximately 25% of mammals are threatened with extinction, a risk that is amplified under climate change. Persistence under climate change is determined by the combined effects of climatic factors on multiple demographic rates (survival, development, reproduction), and hence, population dynamics. To assess species' vulnerability to climate change, we synthesize information from 107 studies, corresponding to 87 mammal species, that quantitatively link climate to multiple demographic rates. We reveal a strong mismatch between the locations of demographic studies and the regions and taxa currently recognized as most vulnerable to climate change. Moreover, the effects of climate change on mammals will operate via complex demographic mechanisms: a vast majority of populations display projected increases in some demographic rates but declines in others. Assessments of population viability under climate

change therefore need to account for multiple demographic responses, and coordinated actions to assess mammal demography holistically should be prioritized.

Introduction

The *ca*. 6,400 extant mammal species can be found in virtually all terrestrial and most aquatic habitats (Jenkins *et al.* 2013). This evolutionary success has been facilitated by the wide range of mammalian life history strategies (Healy *et al*. 2019), which enable them to cope with vastly different climates (Promislow *et al*. 1990). These strategies include extreme examples like male semelparity in some Australian marsupials with very short mating seasons (Fisher *et al.* 2013) or high behavioral plasticity in primates to buffer from the negative effects of environmental variation (Campos *et al*. 2017). This tremendous variation in life history strategies can be captured by differences among organisms in their rates and timing of survival, development, and reproduction (Stearns 1992). It is these demographic rates that determine population growth and thus species persistence.

Important efforts have been made in the last decade to increase the amount of comparative data to understand the variation in demographic rates across mammals (Conde *et al*. 2019). These data have resulted in the broader availability of open-access demographic data on mammal populations (Jones *et al*. 2009; Salguero-Gómez *et al*. 2016). However, we still lack a holistic understanding of how climate drivers simultaneously affect survival, development, and reproduction in mammals worldwide. We do not know whether research quantifying the response of mammal populations to climatic drivers is available for regions most vulnerable to climate change or for the most vulnerable species. Moreover, the complexity of demographic responses to climate remains unknown, despite an emerging consensus that interactions among demographic rates and biotic and abiotic drivers hinder simplistic projections of persistence under climate change (Benton *et al*. 2006; Urban *et al*. 2016). For instance, a negative effect of climate on a specific demographic rate does not necessarily cause a population to go extinct, when another demographic rate responds positively to climate, or when population dynamics are mediated by interactions among climate drivers and density-dependent feedbacks (Reed *et al*. 2013; Paniw *et al*. 2019).

Here, we synthesize our understanding regarding where, which, and how mammal populations respond to climate. We conducted a rigorous review of literature linking multiple demographic rates to climatic drivers, thus capturing the complexity of demographic responses, on 5,856 mammal species with available life-history information (Myhrvold *et al*. 2015). We then linked data from the literature review to information on ecoregion and species' vulnerability to climate change (Beaumont *et al*. 2011; IUCN 2019) to explore (i) whether mammal demographic studies are conducted in ecoregions that are most vulnerable to projected increases in temperature extremes (Q1: *Where*?) (18); (ii) whether demographic responses to projected changes in climate reflect species' extinction risk as determined by the IUCN Red List status of mammals (Q2: *Which species*?); and (iii) through which demographic processes projected changes in climate may show negative and/or positive effects on populations (Q3: *How*?).

Methods

We obtained scientific names of all 5,856 mammal species with available life-history information from the Amniote database (Myhrvold *et al*. 2015). For each species, we searched SCOPUS for studies (published before 2018) that quantified demographic-rate-climate relationships (for the full list of search terms, see WebPanel 1). From any study that matched our search terms, we extracted information on these relationships only if (i) the study linked at least two different demographic rates (*i.e.*, survival, development/growth, or reproduction) to a climatic driver (*i.e.*, any direct or indirect measure of temperature or precipitation); and (ii) the response of a demographic rate to a climatic driver was quantified using statistical methods (*i.e*., excluding qualitative or descriptive studies). In addition, we only considered studies on natural populations of terrestrial mammals, or partially terrestrial mammals (e.g., polar bears), because initial results showed that there were only few climate-related population studies on fully aquatic mammals, which considered distinct climatic drivers (e.g., ocean circulation indices), lacked future projections, and were not easily assigned to specific ecoregions.

From all studies meeting our criteria, we extracted the effect any climatic driver had on age- or stage-specific demographic rates. We grouped these effects as positive (*i.e.,* increased rate), negative (*i.e.*, reduced rate), no effect, or nonlinear (e.g., positive effects at intermediate values and negative at extremes). We also recorded whether climate effects were mediated by other factors (e.g., density, biotic interactions). In studies that indicated future projections of drivers, we recorded whether drivers were projected to increase, decrease, or show nonlinear trends. For the 70% of studies that did not report on projections, we quantified such future projection for climatic variables that depicted direct precipitation and temperature measures (for details, see WebPanel 1). Briefly, we obtained monthly average temperatures and rainfall data as well as maximum and minimum monthly temperatures from 1979-2013 for all relevant study locations using *climatologies at high resolution for the earth's land surface areas* (CHELSA) (Karger *et al*. 2017). We also obtained projections of these variables for 2041-2060 assuming five diverging climate models (WebPanel 1). We then quantified whether a given driver was projected to increase or decrease (95 % CI across the five projection models did not cross historical values) or show no change (95 % CI crossed historical values). From this information, we determined whether a demographic rate would decrease (e.g., positive response to a driver projected to decrease) or increase (e.g., positive response to a driver projected to increase). Unless explicitly stated otherwise in a study, we assumed that demographic rates that were not affected by a climatic variable would not change in the future, and ones that showed nonlinear responses would also likely show nonlinear responses in the future.

A full list of extracted studies and a more detailed description of the extraction protocol and climate modeling can be found in WebPanel 1 and WebTable 1. The multitude of methodological approaches used to study demographic responses (e.g. correlation analyses, structured demographic models, individual-based models) renders a meta-analytical approach impractical.

We determined the vulnerability of global ecoregions to climate change following Beaumont and colleagues (2011), who assessed the likelihood that, by 2070, the “Global 200”, *i.e.*, 238 ecoregions of exceptional biodiversity (Pimm *et al*. 2014), would regularly experience monthly climatic conditions that were extreme in 1961–1990. To characterize ecoregions vulnerable to increases in temperature extremes, we first matched the geographic locations of the studied mammal populations to the geographic extent of the G200 ecoregions. We then characterized temperature vulnerability of the G200 ecoregions that contained the studied mammal populations using the weighted average minimum monthly distance in temperatures (under the A2 climate model ensemble) from the mean of the 1961-1990 baseline (Beaumont *et a*l. 2011). The higher the distance, the more vulnerable an ecoregion. Lastly, to assess a potential mismatch in demographic studies and ecoregion climate vulnerability (Q1: *Where*?), we quantified the proportion of positive, negative, nonlinear, or no-effect responses of demographic rates to any local temperature variable in each G200 ecoregion. This assessment is conservative in that we did not perform it for precipitation; precipitation extremes, although likely to increase in numerous natural systems, were not projected to increase at an ecoregion level (Beaumont *et al*. 2011).

To assess whether demographic responses to projected changes in climate (see below) agree with the International Union for Conservation of Nature and Natural Resources (IUCN) Red List status of mammals (Q2: *Which species?*), we obtained IUCN assessments (including threats) for all species identified in the literature review. We used the R package *rredlist* to access the IUCN Red List database and extract available information on whether the species are listed in the database, and, if so, what status they are assigned to and whether climate change is listed as an existing or potential threat.

Results

We extracted information on climate-demography relationships from 107 studies, for a total of 87 mammal species, that quantified simultaneous responses to climate in at least two different age/stage-specific demographic rates. These studies span 14 biomes, with the exception of tropical and subtropical coniferous forests and mangroves (WebFigure 1). Overall, more studies assess only the direct effects of precipitation (n = 47) than the direct effects of temperature (n = 11) (WebFigure 2); and in 19 of the 107 studies, only indirect effects are assessed via global indices such as the North Atlantic Oscillation (NAO) or El Niño–Southern Oscillation (ENSO). Few studies (10%) test how different climatic drivers interact with one another, approximately half (55%) test for the effects of density dependence on demographic rates, and an additional 20% test for interactions with non-climatic drivers other than population density (e.g. predation, food availability).

In addressing “Q1: *Where*?”, our synthesis reveals that few demographic studies are conducted in ecoregions that are both most biodiverse and most vulnerable to climate change (Olson and Dinerstein 2002). We find that 42 out of the 107 demographic studies were conducted in one of the G200 ecoregions (Fig. 1). However, only 13 of these studies assess the demographic effects of temperature increases, which, unlike precipitation, is projected to become more extreme in all G200 ecoregions (Beaumont *et al*. 2011). In addition, no study has examined the responses of different demographic rates in ecoregions with the highest vulnerability scores (e.g., the Central Congo Basin; darkest red in Fig. 1). Only one study, which includes three primate species, assesses temperature effects in relatively highly vulnerable G200 ecoregions; and finds no effects (Fig. 1 insert) likely due to the primates’ behavioral and physiological flexibility before climate variation (Campos *et al*. 2017).

In addition to an ecoregion bias, in answering “Q2: *Which species*?”, we highlight that demographic analyses have taxonomic bias. Studies linking multiple demographic rates to climatic drivers are primarily performed in regions with a relatively low mammal richness and on species that are not currently vulnerable to climate change (Fig. 2), based on IUCN classifications. Indeed, the IUCN has identified at least 17% of listed vertebrates to be sensitive to climate change, *i.e.*, decreasing in numbers or losing habitat under changes in temperature and precipitation regimes due to elevated atmospheric CO_2 levels (Marris 2008). Our synthesis reveals that only 4% of all mammals assessed as climate sensitive by the IUCN have detailed studies linking demography to climate (*i.e.*, 13% of studies we assessed). Interestingly, the proportion of demographic rates per study that will decline under projected changes in climatic drivers (0.31, ± 0.10 S.E.) is highest for species that have been flagged by the IUCN as climate sensitive. However, this proportion is followed closely by species for which climate change is not considered a threat by the IUCN (Fig. 2 insert).

In addressing "Q3: *How*?", our synthesis reveals that multi-directional demographic responses to climate are prevalent. Only eight of the 107 studies report unidirectional (all positive) responses of demographic rates to climatic drivers, while 11 studies find no effect of climate on any demographic rate (WebFigure 3). For the vast majority of species, the direction of observed (79%) and projected (75%) demographic responses to climate vary depending on the demographic rate or age/stage being considered (examples in Fig. 3 insert); and on interactions among climatic and non-climatic drivers, with interactions often mediated by density feedbacks (WebFigure 3). In addition, 13 studies assess the effects of climate on population growth rates in addition to underlying demographic rates (WebFigure 3, WebTable 1). These examples show that population responses are not readily predictable from a single demographic rate when multiple climatic drivers and their interactions with biotic drivers affect demography.

Conclusions

Our synthesis suggests that gaining a global understanding of the mammals that are most vulnerable to climate-driven extinction will require filling important knowledge gaps. Studies on climate effects across the whole life cycle of populations are needed in many biodiversity hotspots that also highly susceptible to climate change (Beaumont *et al*. 2011). Many of these ecoregions also face strong pressures on biodiversity from direct human activities (Venter *et al*. 2016). A majority of demographic studies where multiple demographic rates are linked to climate in vulnerable ecoregions and elsewhere nevertheless does not account for interactions with nonclimate drivers. These omissions may bias estimates of population viability as population dynamics are typically driven by compound effects of interacting climatic and non-climatic drivers (Benton *et al*. 2006), which are projected to become more extreme under climate change (Zscheischler *et al*. 2018).

Our analysis also reveals that studies assessing responses to climate across different demographic rates are required for most mammals considered climate-sensitive by the IUCN, allowing this threat to be understood and potentially mitigated through conservation. On the other hand, given that a large number of mammals not considered to be climate sensitive may actually show strong negative demographic responses to climate change, our results support the need for current IUCN efforts to re-evaluate the importance of climate as an extinction threat to mammals (Foden and Young 2016).

By focusing on studies that have assessed several demographic responses to climate, we necessarily limited the number of taxa in our review. In fact, we identified at least 111 more studies on 68 additional species that only assessed climatic effects on single demographic rates. We stress here that we do not question the validity of such studies when population dynamics can be accurately predicted from the changes in one key demographic rate. However, population responses to climate are typically determined by the covariation among multiple demographic rates, which itself is often mediated by a myriad of interacting biotic and abiotic factors, (e.g., Reed *et al*. 2013). For instance, impalas (*Aepyceros melampus*), which the IUCN characterizes as threatened by drought (WebTable 1), may show positive or negative responses in survival and reproductive success under rainfall scarcity depending on the seasonal patterning of rainfall and population density (Ogutu *et al*. 2012). Similarly, meerkats (*Suricata suricatta*), which currently face no threats according to the IUCN, show nonlinear, *i.e.*, both positive and negative, responses to precipitation across several critical demographic rates due to social interactions and density feedbacks (Ozgul *et al*. 2014). Therefore, as a cooperative breeder, meerkats may be vulnerable to increases in seasonal climatic extremes that decrease group densities (Paniw *et al*. 2019). Such complex demographic responses make it challenging to project species' fates under climate change because the future of populations cannot be accurately determined from single demographic rates (Urban *et al.* 2016).

As consistently negative demographic responses to climate change are only relatively common in species the IUCN flagged as climate sensitive, our results suggest that complexity of demographic responses may buffer populations from adverse climate effects (González-Suárez and Revilla 2013). Therefore, despite the challenges involved in collecting long-term demographic parameters across the entire life cycle (Foden and Young 2016), the mechanistic insights gained from such parameters will be invaluable to understand the drivers of biodiversity loss under climate change (Urban *et al*. 2016).

Mammals are key ecosystem engineers, frequent apex predators, and providers of important ecosystem services, (e.g., Wallach *et al*. 2017; Poulsen *et al*. 2018). Future dynamics of mammal populations can therefore determine overall ecosystem change (Zarnetske *et al*. 2012). Our current mechanistic knowledge on mammal responses to climate change would benefit from strategic studies that fill the knowledge gaps identified here. Along with recent calls for a renewed global effort to collect natural-history information (Urban *et al*. 2016), we advocate for a coordinated effort to collect and model demographic responses to climate across the entire life cycle of species, particularly in vulnerable ecoregions such as moist forests in the Congo Basin or mangroves in Madagascar.

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Data availability

The data that support the findings in this study are available in the Supplementary Online Materials, WebTable 1.

Code availability

The code that supports the findings in this study is available in the Supplementary Online Materials, `climate_change_analyses_mammal_review.R`.

Author Contributions

MP, TJ, GR, and RS-G devised the overall manuscript. MP and TJ designed the literature review protocol, which was then implemented by MP, TJ, GR, CRA, SL, AM, JC, NSG, JMB, and AP. The climatic data were derived by AC. The first draft of the manuscript was written by MP and RS-G, and all co-authors contributed to the final manuscript. See Table S2 for further specifics regarding task contributions.

References

Beaumont LJ, Pitman A, Perkins S, *et al.* 2011. Impacts of climate change on the world's most exceptional ecoregions. *Proc Natl Acad Sci USA* **108**: 2306–11.

Benton TG, Plaistow SJ and Coulson TN. 2006. Complex population dynamics and complex causation: devils, details and demography. *Proc Biol Sci* **273**: 1173–81.

Campos FA, Morris WF, Alberts SC, *et al*. 2017. Does climate variability influence the demography of wild primates? Evidence from long-term life-history data in seven species. *Glob Change Biol* **23**: 4907–21.

Conde DA, Staerk J, Colchero F, *et al*. 2019. Data gaps and opportunities for comparative and conservation biology. *Proc Natl Acad Sci USA* **116**: 9658–64.

Fisher DO, Dickman CR, Jones ME, *et al*. 2013. Sperm competition drives the evolution of suicidal reproduction in mammals. *Proc Natl Acad Sci USA* **110**: 17910–14.

Foden WB and Young BE. 2016. *IUCN SSC Guidelines for Assessing Species' Vulnerability to Climate Change*. UCN Cambridge, England and Gland, Switzerland.

González-Suárez M and Revilla E. 2013. Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecol Lett* **16**: 242–51.

Healy K, Ezard THG, Jones OR, *et al*. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nat Ecol Evol* **3**: 1217–24.

IUCN (International Union for Conservation of Nature). 2019. The IUCN red list of threatened species. http://www.iucnredlist.org. Viewed 25 Jan 2020.

Jenkins CN, Pimm SL and Joppa L N. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proc Natl Acad Sci USA* **110**: E2602–10.

Jones KE, Bielby J, Cardillo M, *et al*. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology* **90**: 2648–48.

Marris E. 2008. Pre-emptive strike: outwitting extinction. *Nat Clim Change* **1**: 140–41.

Myhrvold NP, Baldridge E, Chan B, *et al*. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. *Ecology* **96**: 3109.

Ogutu JO, Piepho HP and Kanga E. 2012. Dynamics of an insularized and compressed impala population: rainfall, temperature and density influences. *Open J Ecol* **5**: 1–17.

Olson DM and Dinerstein E. 2002. The Global 200: Priority ecoregions for global conservation. *Ann Mo Bot Gard* **89**: 199–224.

Ozgul A, Bateman AW, English S, *et al*. 2014. Linking body mass and group dynamics in an obligate cooperative breeder. *J Anim Ecol* **83**: 1357–66.

Paniw M, Maag N, Cozzi G, *et al.* 2019. Life history responses of meerkats to seasonal changes in extreme environments. *Science* **363**: 631–35.

Pimm SL, Jenkins CN, Abell R, *et al*. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**: 1246752.

Poulsen JR, Rosin C, Meier A, *et al*. 2018. Ecological consequences of forest elephant declines for Afrotropical forests. *Conserv Biol* **32**: 559–67.

Promislow DEL and Harvey PH. 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. *J Zool* **220**: 417–37.

Reed TE, Grøtan V, Jenouvrier S, *et al*. 2013. Population growth in a wild bird is buffered against phenological mismatch. *Science* **340**: 488–91.

Salguero-Gómez R, Jones OR, Archer CR, *et al*. 2016. COMADRE: a global data base of animal demography. *J Anim Ecol* **85**: 371–84.

Stearns SC. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Urban MC, Bocedi G, Hendry AP, *et al*. 2016. Improving the forecast for biodiversity under climate change. *Science* **353**: aad8466.

Venter O, Sanderson EW, Magrach A, *et al*. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Comm* **7**: 12558.

Wallach AD, Dekker AH, Lurgi M, *et al*. 2017. Trophic cascades in 3D: network analysis reveals how apex predators structure ecosystems. *Methods Ecol Evol* **8**: 135–42.

Zarnetske P L, Skelly DK and Urban MC. 2012. Biotic multipliers of climate change. *Science* **336**: 1516–18.

Zscheischler J, Westra S, van den Hurk BJJM, *et al.* 2018. Future climate risk from compound events. *Nat Clim Change* **8**: 469–77.

Supplementary Information is available in the online version of the paper.

Figure legends

Figure 1. Global distribution of 107 mammal studies (grey points) that have comprehensively assessed demographic responses to climate across the species' life cycles. Point size indicates number of relationships between climatic drivers and age/stage-specific demographic rates (survival, development, and/or reproduction). Red-scale map background indicates projected climate-change vulnerability for the most biodiverse (G200) ecoregions, with redder colors indicating higher increase in extreme temperatures. Left insert shows number of demographic rates decreasing (-), not changing (0), or increasing (+) under increasing temperatures as function of ecoregion vulnerability. Green shading on insert indicates total number of demographic rates linked to temperature per ecoregion vulnerability level.

Figure 2. Global distribution of mammals (points) with available information on climate-demography relationships. Point and bar colors indicate levels of threat assessment by the IUCN (No IUCN - species not assessed; No T - species assessed and currently faces no threats; No CT - climate change not considered a threat; CT - climate change considered a threat). Darker background on the map indicates higher mammal richness (number of species). Bottom-left insert displays the mean proportion of demographic rates per mammal population ± S.E. (error bars) that will decrease under projected climate change in different IUCN categories. Total number of

populations with at least one decreasing rate per threat level are indicated above the bars. Species highlighted in Figure 3 are mapped here.

Figure 3. Summary of responses of demographic rates under projected changes in climate across IUCN threat categories (left panel). The proportion of studied populations (out of total number indicated) is shown where the same (within) demographic rate is projected to increase or decrease (+/-) depending on the age/stage modeled; or where a positive response in one rate but negative in another rate (among) are projected. Categories include No IUCN - species not assessed; No T - species assessed and currently faces no threats; No CT - climate change is not considered a threat; CT - climate change is considered a threat). Detailed responses for 11 example species highlighting the full spectrum of responses are shown in the right panel. Demographic rates include survival (S), probability of reproducing and reproductive output (R), and growth and development (G), which can show only positive (+), only negative (-), nonlinear (NL; both positive and negative), or no (0) responses in the future. From top left to bottom right, the species include Soay sheep (*Ovis aries*), agile antechinus (*Antechinus agilis*), yellow-bellied marmot (*Marmota flaviventer*), meerkat (*Suricata suricatta*), pika (*Ochotona curzoniae*), long-tailed wattled bat (*Chalinolobus tuberculatus*), Milne-Edwards's sifaka (*Propithecus edwardsi*), northern muriqui (*Brachyteles hypoxanthus*), Saiga antelope (*Saiga tatarica*), impala (*Aepyceros melampus*), and black-flanked rock-wallaby (*Petrogale lateralis*).

Figure 1

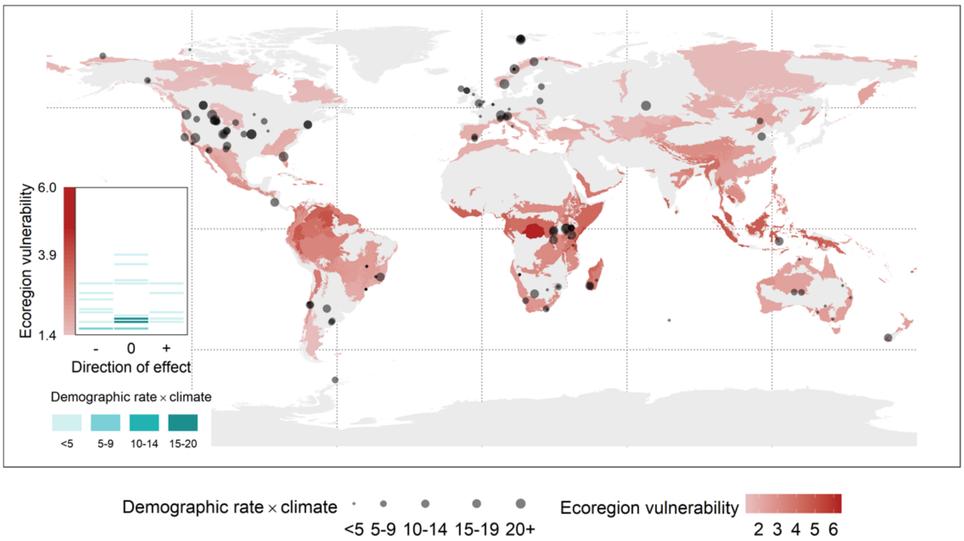
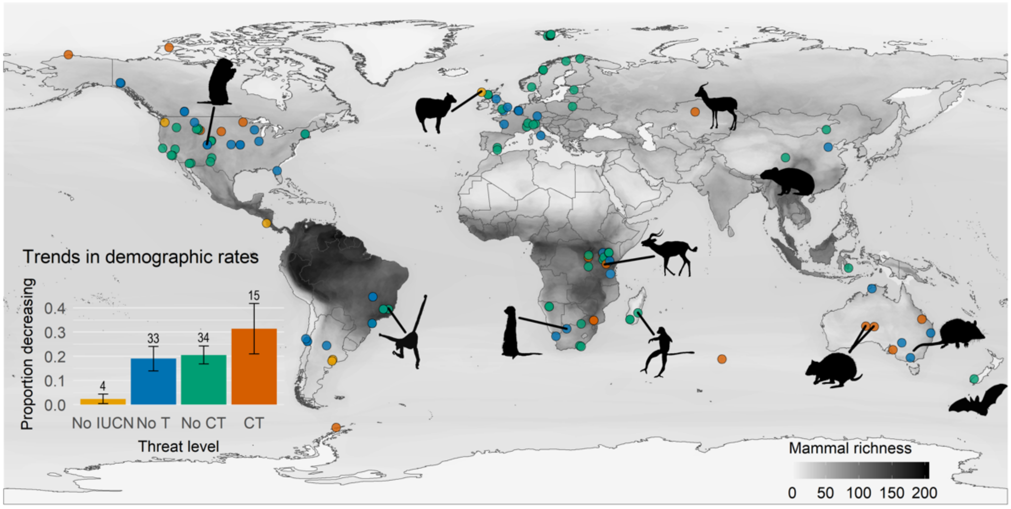
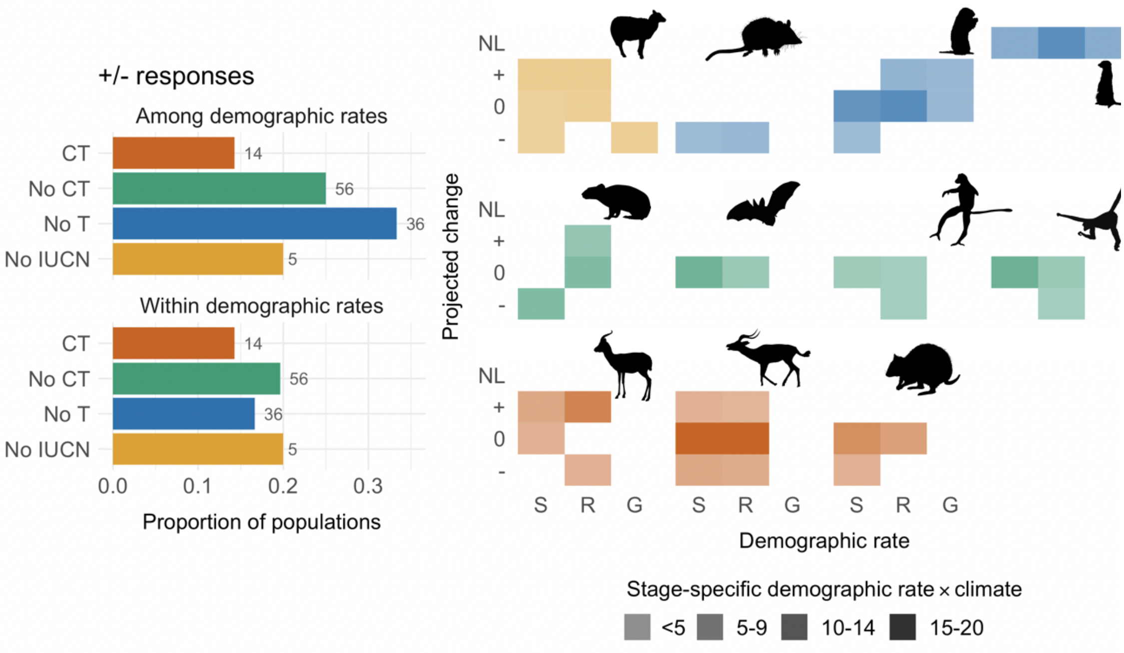


Figure 2



403 **Figure 3**



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5.3 Supporting information

Supporting Information S1 for

The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis

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Detailed Extraction Protocol and Data Description

For each mammal species *i* with available life-history information, we searched SCOPUS for studies (published before 2018) where the title, abstract, or keywords contained the following search terms:

> *Scientific species name*$_i$ AND (demograph* OR population OR life-history OR "life history" OR model) AND (climat* OR precipitation OR rain* OR temperature OR weather) AND (surv* OR reprod* OR recruit* OR brood OR breed* OR mass OR weight OR size OR grow* OR offspring OR litter OR lambda OR birth OR mortality OR body OR hatch* OR fledg* OR productiv* OR age OR inherit* OR sex OR nest* OR fecund* OR progression OR pregnan* OR newborn OR longevity).

We used the R package *taxize* (Chamberlain and Szöcs 2013) to resolve discrepancies in scientific names or taxonomic identifiers and, where applicable, searched SCOPUS using all scientific names associated with a species in the Integrated Taxonomic Information System (ITIS; http://www.itis.gov).

We did not extract information on demographic-rate-climate relationships if:

- A study reported on single age- or stage-specific demograpihc rates (e.g., Albon *et al*. 2002; Rézoiki *et al*. 2016)
- A study used an experimental design to link demographic rates to climate variation (e.g., Cain *et al*. 2008)
- A study considered the effects of climate only indirectly or qualitatively. In most cases, this occurred when demographic rates differed between seasons but were not linked explicitly to climatic factors driving these differences (e.g., de Silva *et al*. 2013; Gaillard *et al*. 2013).

We included several studies of the same population as different studies assessed different climatic variables or demographic rates or spanned different years (e.g., for *Rangifer tarandus platyrhynchus*, Albon *et al*. 206; Douhard *et al*. 2016).

Lastly, we note that we can miss a potentially relevant study if our search terms were not mentioned in the title, abstract, or keywords. To our knowledge, this occurred only once, for *Mastomys natalensis* (we included the relevant study [Leirs *et al*. 1997] into our review after we were made aware that it assesses climate-demography relationships in the main text).

Description of key collected data

From all studies quantitatively assessing climate-demography relationships, we extracted the following information:

a) Geographic location - The center of the study area was always used. If coordinates were not provided in a study, we assigned coordinates based on the study descriptions of field sites and data collection.
b) Terrestrial biome - The study population was assigned to one of 14 terrestrial biomes (Olson *et al.* 2001) corresponding to the center of the study area. As this review is focused on general climatic patterns affecting demographic rates, specific microhabitat conditions described for any study population were not considered.

c) Climatic driver - Drivers linked to demographic rates were grouped as either local precipitation & temperature indices or global indices (e.g., ENSO, NAO). The temporal extent (e.g., monthly, seasonal, annual, etc.) and aggregation type (e.g., minimum, maximum, mean, etc.) of drivers was also noted.

d) Demographic rate modeled - To facilitate comparisons, we grouped the demographic rates into either survival, reproductive success (*i.e.*, whether or not reproduction occurred), reproductive output (*i.e.*, number or rate of offspring production), growth (including stage transitions), or condition that determines development (*i.e.,* mass or size).

e) Stage or sex modeled - We retrieved information on responses of demographic rates to climate for each age class, stage, or sex modeled in a given study.

f) Driver effect - We grouped effects of drivers as positive (*i.e.,* increased demographic rates), negative (*i.e.*, reduced demographic rate), no effect, or nonlinear (e.g., positive effects at intermediate values and negative at extremes).

g) Driver interactions - We noted any density dependence modeled and any non-climatic covariates included in the demographic-rate models assessing climatic effects.

h) Future projections of climatic driver - In studies that indicated projections of drivers under climate change, we noted whether drivers were projected to increase, decrease, or show nonlinear trends. For studies that provided no information on climatic projections, we quantified projections as described in *Detailed description of climate-change projections* below (see also `climate_change_analyses_mammal_review.R`).

Protocol summary

Data were extracted from papers by a team of digitizers (see Table 1 below), each of whom worked independently on a randomly assigned collection of species. A formatted data-sheet was provided to facilitate consistent and standardized data extraction. Once individuals had collected data, the resulting dataset was error checked in a number of ways. For example, digitizers randomly checked 10% of papers in the database entered by colleagues, to ensure that outputs from two different digitizers were consistent. Error-checkers also ensured that there were no duplicated manuscripts recorded (this could conceivably happen if a paper modelled more than one species and digitizers extracted data for all species studied in a particular manuscript) and also that all data were entered in a standardized format. Here, we describe all of the data that were collected, and how each item of data was defined.

Detailed data description

1. *Location data*
    a. *Latitude and longitude*

The latitude and longitude of a particular study site (as reported in the manuscript) were recorded in decimal degrees using the WGS84 global projection. Notes were also made on how the location was described in the paper, *i.e.* if the location provided represented the middle of a study site, or how latitude and longitude were calculated for migratory species. If latitude and longitude were not reported in the original manuscript, the digitizers used the verbal description of the study site (e.g. nearest town, center of national park etc. where the study was conducted) to estimate these values. Such an approximation of study location did not affect our analyses and conclusions, which were based on broad-scale ecoregion comparisons and on climate data that were interpolated over a relatively large grid of approximately 1 km^2.

    b. *Biomes and ecoregions*

We obtained georeferenced maps of terrestrial biomes and ecoregions from the World Wildlife Fund (Olson *et al*. 2001). Each location identified in our review could therefore be placed into a biome that consisted of one or more ecoregions, some of which correspond to highly diverse G200 ecoregions. Terrestrial biome categories included: **TMB** – tropical and subtropical moist broadleaf forests; **TDB** – tropical and subtropical dry broadleaf forests; **TSC** – tropical and subtropical coniferous forests; **TBM** – temperate broadleaf and mixed forests; **TCF** – temperate coniferous forests; **BOR** – boreal forests / taiga; **TGV** – tropical and subtropical grasslands, savannas and shrublands; **TGS** – temperate grasslands, savannas and shrublands; **FGS** - flooded grasslands and savannas; **MON** – montane grasslands and shrublands; **TUN** – tundra; **MED** – Mediterranean forests, woodland and scrubs; **DES** – deserts and xeric shrublands; **MAN** – mangroves. Definitions for each of these biomes as well as all ecoregions can be found at http://wwf.panda.org/about_our_earth/ecoregions/ecoregion_list/.

2. Climatic Data

a. Climatic Drivers

Climatic drivers were divided into the following categories: **P** - any measure of precipitation; **T** - any measure of temperature; **PT -** measures such as drought or icing that reflect both temperature and precipitation. Some climatic drivers were variables derived from raw measures of precipitation and temperature. These variables were described as in the reviewed papers and include **NAO -** Northern Atlantic Oscillation, **ENSO** - El Niño–Southern Oscillation; **SAM -** Southern Annular Mode; **SOI** - Southern Oscillation Index, **PDSI** - Precipitation and Surface Air Temperature and **PDO** - Pacific Decadal Oscillation. A detailed description of each of the climatic drivers included in the dataset was also recorded, to facilitate error checking and data-standardization.

b. Temporal Aggregation

How climatic data were aggregated in statistical models was recorded, with options being: **D** - daily; **S** - seasonal; **M** - monthly; **A** - annual.

c. Aggregation Methods

The method used to aggregate climatic data was recorded with options including **sum** - the sum of all climatic values; **min** - the minimum observed value; **max** - the maximum observed value;

mean - the average value; **SD -** standard deviation in climatic values; **range -** difference between minimum and maximum observed values; **length -** number of days, or growing degree days.

3. Response Traits

a. Demographic rates

The studies that feature in the dataset quantified demographic rates in different ways. Accordingly, we grouped the rates featuring in each paper as being associated with survival, reproductive success, reproductive output, growth/development, condition, or population growth. Here, we outline how we assigned traits from individual studies to each of these classes.

Survival - Both mortality rates and survival rates feature in our database. However, to ensure that these rates were comparable between studies we reported the sign of any effect as being appropriate for a measure of survival, *i.e.* an environmental variable that increased mortality risk, was recorded in our dataset as reducing survival.

Reproductive Success and Output - Studies quantifying reproduction may have recorded the probability of reproduction, number of offspring, reproductive success, number of litters, birth rate, fecundity, reproductive rate, pregnancy or transition into reproductive state. For the purpose of our analyses, any binary variable that defined whether a reproductive event occurred or not, was recorded as a measure of ***Reproductive Success***, while any measure of how many, or how frequently offspring were produced was classed as ***Reproductive Output****.*

Growth/Development - Variables that quantified individual growth rates, development or generation time were included as measures of growth.

Condition - In some cases condition was quantified explicitly using a species-specific parameter, but in other cases mass or body size was measured.

b. Stage, State or Sex Modelled

Digitizers recorded which life-stage (i.e. juvenile, adult), sex and state (e.g. individual size for IPMs) was modelled, using the description provided by the authors in the manuscript. If an unstructured population model was used, this was recorded as “unstructured”.

c. Direction of effect

Digitizers recorded if the climatic driver has a negative effect on the demographic rate (**neg**), a positive effect (**pos**), a nonlinear effect (**nonlinear**) or no effect **(noe**).

d. Duration of Study

The number of years that data were collected was recorded.

4. Model Details

To understand the nature of the models collected in our data-base, for example, how often existing data quantifies interactions between climatic variables, the details of the model were recorded as described below.

a. Density Dependence

Digitizers recorded whether data dependence was modelled (binary variable, **yes** or **no**).

b. Indirect Effect of Driver

Digitizers recorded if indirect effects, e.g., path analyses, were tested for in the model (binary variable, **yes** or **no**).

c. Non-linear Effect of Driver

If a climatic driver had a non-linear effect on the demographic rate, the nature of that effect was described here, with examples including **quadratic**, **lag** or **other**.

d. Interaction with Other Climatic Driver(s)

Were interactions considered between climatic drivers (binary variable, **yes** or **no**)?

e. Interaction with Other Non-Climatic Driver(s)

Were interactions considered between climatic drivers and other variables not related to climate? Digitizers recorded **yes** or **no**

f. Non-Climatic Drivers

Where relevant, a description of the non-climatic driver(s) modelled was recorded as concisely as possible.

g. Future Driver Direction

If described in a paper, we noted how the climatic driver modelled was expected to change under current climatic change models. Options included **increase**, **decrease**, **nonlinear**, or **no change**.

Detailed description of climate-change projections

For studies which did not report on "*future projections of climatic driver*" (70% of studies), we quantified such future projection for climatic variables that depicted direct precipitation and temperature measures. For global indices such as ENSO or NAO, future projections could not be obtained (with the exception of the ones explicitly discussed in a given study), as such projections are either lacking or extremely complex and uncertain (Stevenson 2012; Chen *et al*. 2017; Wang *et al*. 2017). All analyses can be replicated using the R script `climate_change_analyses_mammal_review.R`. To project future changes in temperature and precipitation, we obtained monthly average temperatures and rainfall data as well as maximum and minimum monthly temperatures from 1979-2013 for all relevant study locations from CHELSA (Karger *et al*. 2017). We averaged these historical climate records for each month and calculated standard deviation across months, which we could then link to studies that assessed the effects of such deviations. We also obtained monthly projected values of theses variables averaged from 2041 to 2060. We obtained values from five diverging climate models that used different methods for projections assuming a representative concentration pathway of 4.5 W/m^2 (http://chelsa-climate.org/future/).

Figure S1.1 (a) Geographic location of the 107 publications examined in this study that have explicitly evaluated the effect of climate change on mammal population dynamics. (b) Representation of these studies and (c) proportion of mammal species that are endangered (EN) or critically endangered (CR; IUCN Red List of Threatened Species) aggregated by terrestrial biome. TMB: Tropical and Subtropical Moist Forests; TDB: Tropical and Subtropical Dry Forests; TSC: Tropical and Subtropical Coniferous Forests; TBM: Temperate Broadleaf and Mixed Forests; TCF: Temperate Coniferous Forests; BOR: Boreal Forests/Taiga; TGV: Tropical and Subtropical Grasslands, Savannas, and Shrublands; TGS: Temperate Grasslands, Savannas, and Shrublands; FGS: Flooded Grasslands and Savannas; MON: Montane Grasslands and Savannas; TUN: Tundra; MED: Mediterranean Forests, Woodlands, and Shrubs; DES: Deserts and Xeric Shrublands; MAN: Mangrove. Plot in (c) depicts the average (± SE) proportion across polygons classified as a given biome and standardized by polygon area.

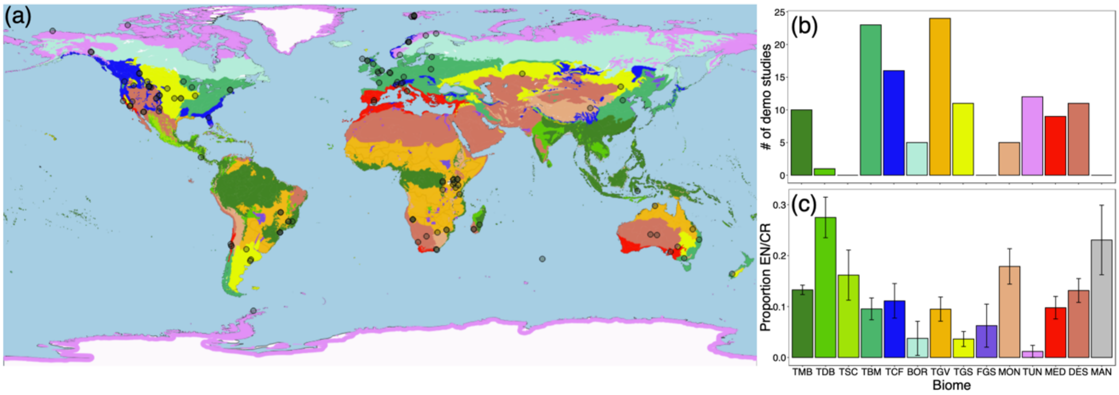

Figure S1.2 Venn diagram representing (area) the number of studies included in our literature review that explicitly linked mammal demographic responses to precipitation (cyan), temperature (red) or both (purple).

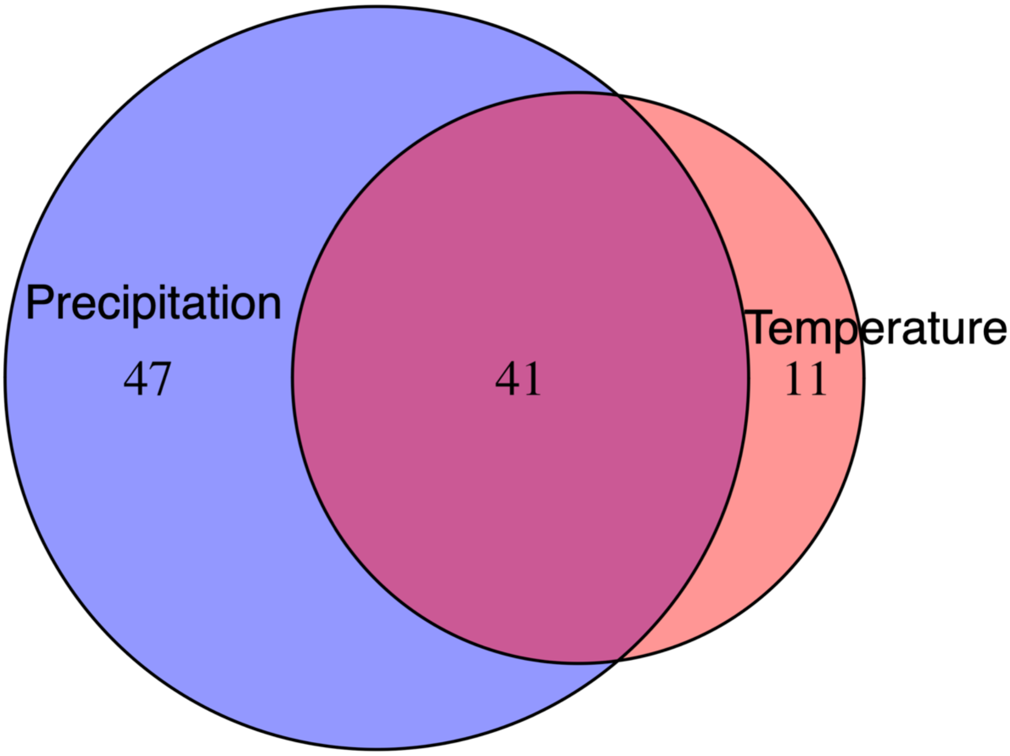

Figure S1.3 Observed (extracted from demographic studies) and projected responses of demographic rates for all mammal species reviewed. Species are sorted by the IUCN threat categories: least concerned (LC), vulnerable (VU), near-threatened (NT), endangered (EN), critically endangered (CR). The topmost species have not been assessed (NL) by the IUCN. Demographic rates include survival (S), probability of reproducing (R), reproductive output (#O), growth and development (G), and population growth (L), which increase (+), decrease (-), or show multidirectional (MD; increase for one life-cycle stage or range of climate and decrease for another) or no (0) responses. Demographic rates for which future changes under projected climate change could not be obtained because these rates were modelled as functions of global indices (e.g., ENSO) that are difficult to project are plotted in beige (right plot). Repetition of species names occurs because several publications assessed climate-demography relationships for some species (e.g. *Ovis aries* or *Rangifer tarandus*).

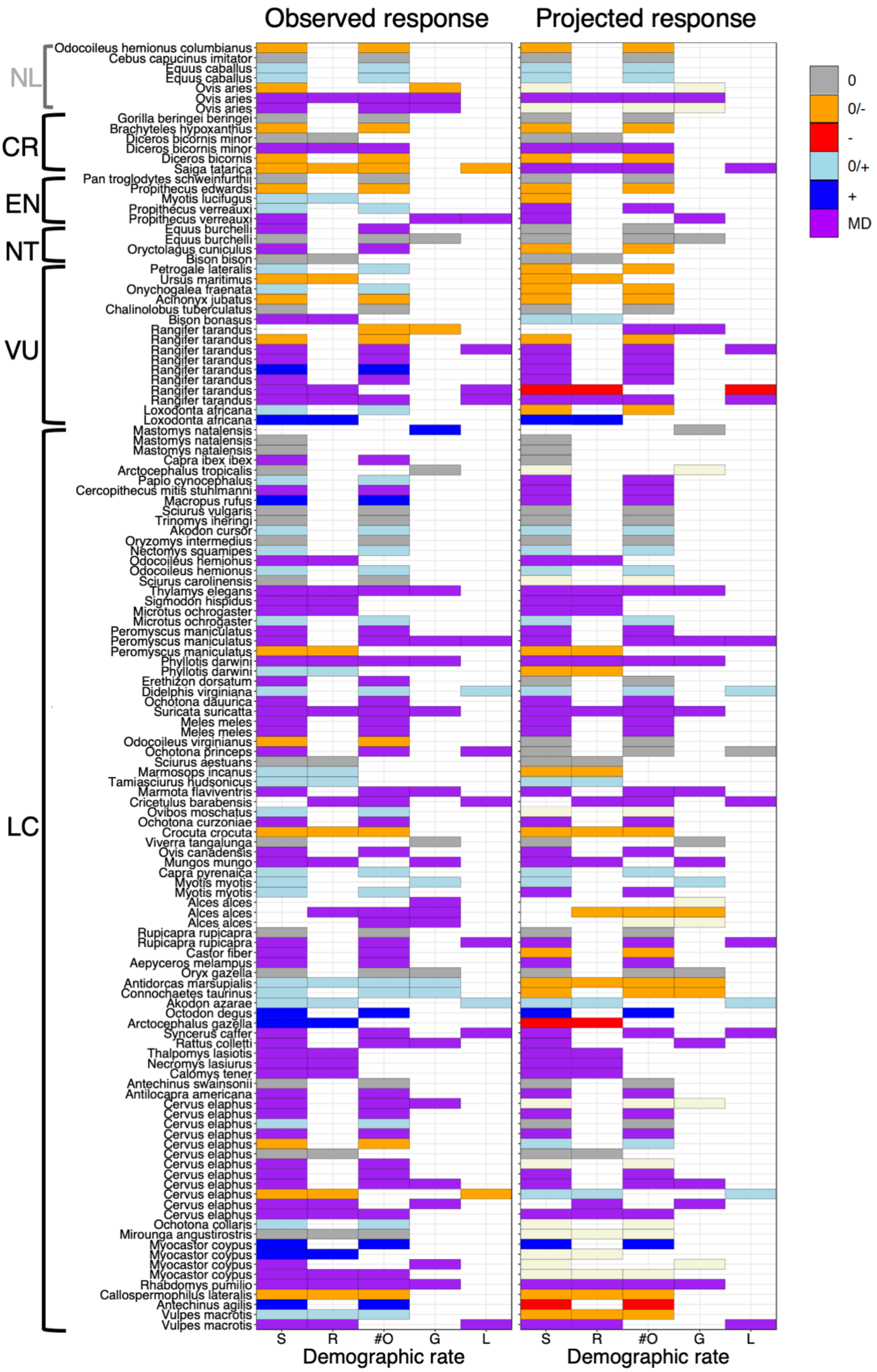
Observed response
Projected response
NL
CR
EN
NT
VU
LC
Odocoileus hemionus columbianus
Cebus capucinus imitator
Equus caballus
Equus caballus
Ovis aries
Ovis aries
Ovis aries
Gorilla beringei beringei
Brachyteles hypoxanthus
Diceros bicornis minor
Diceros bicornis minor
Diceros bicornis
Saiga tatarica
Pan troglodytes schweinfurthii
Propithecus edwardsi
Myotis lucifugus
Propithecus verreauxi
Propithecus verreauxi
Equus burchelli
Equus burchelli
Oryctolagus cuniculus
Bison bison
Petrogale lateralis
Ursus maritimus
Onychogalea fraenata
Acinonyx jubatus
Chalinolobus tuberculatus
Bison bonasus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Loxodonta africana
Loxodonta africana
Mastomys natalensis
Mastomys natalensis
Mastomys natalensis
Capra ibex ibex
Arctocephalus tropicalis
Papio cynocephalus
Cercopithecus mitis stuhlmanni
Macropus rufus
Sciurus vulgaris
Trinomys iheringi
Akodon cursor
Oryzomys intermedius
Nectomys squamipes
Odocoileus hemionus
Odocoileus hemionus
Sciurus carolinensis
Thylamys elegans
Sigmodon hispidus
Microtus ochrogaster
Microtus ochrogaster
Peromyscus maniculatus
Peromyscus maniculatus
Peromyscus maniculatus
Phyllotis darwini
Phyllotis darwini
Erethizon dorsatum
Didelphis virginiana
Ochotona dauurica
Suricata suricatta
Meles meles
Meles meles
Odocoileus virginianus
Ochotona princeps
Sciurus aestuans
Marmosops incanus
Tamiasciurus hudsonicus
Marmota flaviventris
Cricetulus barabensis
Ovibos moschatus
Ochotona curzoniae
Crocuta crocuta
Viverra tangalunga
Ovis canadensis
Mungos mungo
Capra pyrenaica
Myotis myotis
Myotis myotis
Alces alces
Alces alces
Alces alces
Rupicapra rupicapra
Rupicapra rupicapra
Castor fiber
Aepyceros melampus
Oryx gazella
Antidorcas marsupialis
Connochaetes taurinus
Akodon azarae
Octodon degus
Arctocephalus gazella
Syncerus caffer
Rattus colletti
Thalpomys lasiotis
Necromys lasiurus
Calomys tener
Antechinus swainsonii
Antilocapra americana
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Cervus elaphus
Ochotona collaris
Mirounga angustirostris
Myocastor coypus
Myocastor coypus
Myocastor coypus
Myocastor coypus
Rhabdomys pumilio
Callospermophilus lateralis
Antechinus agilis
Vulpes macrotis
Vulpes macrotis
S
R
#O
G
L
Demographic rate
S
R
#O
G
L
Demographic rate
0
0/-
-
0/+
+
MD

Table S1.1 List of all extracted information on demographic studies that assessed responses to climatic drivers in at least two vital rates. Available as a text file upon publication on Dryad (doi to be filled). Currently available as *mammal_review_extracted_studies.csv*

Table S1.2 Extended task contribution by each author in this manuscript (ms)

Author	Design extraction protocol	Lead review	Write R code to facilitate review	Manage review tasks	Perform review	Error checking	Standardize results	Conceptualize ms (main questions)	Perform analyses for ms	Write ms	Revise ms
MP	X	X	X	X	X	X	X	X	X	X	X
TJ	X	X	X	X	X	X			X		X
CRA	X				X	X	X	X		X	X
GR					X		X	X	X		X
SL			X	X	X				X		
AC				X					X		X
JC-C	X				X			X			X
JMB					X						X
AM					X						X
DZC								X			X
AO								X			X
ORJ			X					X			X
JHB								X			X
APB								X			X
AP					X	X					
NSG					X			X			X

TMK	X			X				X			X
RS-G				X				X		X	X

Additional references

Albon SD, Irvine RJ, Halvorsen O, *et al*. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Glob Change Biol* **23**: 1374-89.

Albon SD, Stien A, Irvine RJ, *et al*. 2002. The role of parasites in the dynamics of a reindeer population. *Proc Biol Sci* **269**: 1625-32.

Cain JW, Krausman PR, Morgart JR, *et al*. 2008. Responses of desert bighorn sheep to removal of water sources. *Wildl Monog*r **171**: 1-32.

Chamberlain SA and Szöcs E. 2013. taxize: taxonomic search and retrieval in R. *F1000Res*. **2**: 191.

Chen C, Cane MA, Wittenberg AT, *et al*. 2017. ENSO in the CMIP5 Simulations: Life Cycles, Diversity, and Responses to Climate Change. *J Clim* **30**: 775–801.

de Silva S, Webber CE, Weerathunga US, *et al*. 2013. Demographic variables for wild Asian elephants using longitudinal observations. *PLoS ONE* **8**: e82788.

Douhard M, Loe LE, Stien A, *et al*. 2016. The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. *Proc R Soc B* **283**: 20161760.

Gaillard JM, Hewison M, Klein AJ, *et al*. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecol Lett* **16**: 48-57.

Leirs H, Stenseth NC, Nichols JD, *et al.* 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature*, **389**: 176-180.

Olson DM, Dinerstein E, Wikramanayake ED, *et al*. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* **51**: 933–38.

Rézouki C, Tafani M, Cohas A, *et al.* 2016. Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. *J Anim Ecol* **85**: 761-73.

Stevenson SL. 2012. Significant changes to ENSO strength and impacts in the twenty-first century: Results from CMIP5. *Geophys Res Lett* **39**.

Wang L, Ting M and Kushner PJ. 2017. A robust empirical seasonal prediction of winter NAO and surface climate. *Sci Rep* **7**: 279.

Chapter 6

General discussion

6.1 Summary of thesis achievements

The aim of this thesis was to investigate limitations to effective conservation demography that arise from incomplete and biased demographic data and from limited understanding of how life cycle processes and life history shape demographic responses. To explore these restrictions I used a variety of modelling techniques, drawing on core life history and conservation modelling principles. The combination of theory and modelling allowed me to address four fundamental questions.

In Chapter 2, I developed a novel modelling framework to explore constraints imposed by long-term monogamous pair bonds on population performance in long-lived species. This work addressed the typical use of female-based models in conservation and thus the question of whether ignoring interactions between males and females constrains our understanding of conservation priorities. I applied classical sensitivity analysis and transient analysis in a symmetric two-sex demographic framework in which an explicit representation of individual quality determined individual and pair-level processes of pairing and divorce. This framework enabled me to analyse the effects of pairing and divorce in long-lived birds with strong monogamous pair bonds and to explore the demographic and population-level consequences of interactions between life history and pairing and divorce dynamics. I found that both long- and short-term dynamics were largely insensitive to pairing, pair quality and divorce, and that this pattern was similar across alternative life history strategies corresponding to generally long-lived monogamous species. While the assumptions I made can be varied and customised for specific systems, the results suggest that, in populations with nearly sex-symmetric demography, the use of female only models remains an expedient approach for many conservation problems.

In Chapter 3, I evaluated the use of phylogenetic imputation to fill gaps in demographic analysis, addressing the issue of incomplete and biased demographic data that has an impact on many species of conservation concern. Accurate demographic data is vital for parameterising population models for demographic analyses but formal methods for estimating missing vital rates are lacking. These data gaps make it challenging to apply conservation demographic analyses to and estimate key demographic metrics for the most at-risk species. Here, I explored whether standardised avian vital rates can be estimated accurately using phylogenetic imputation and whether estimates of demographic metrics such as generation time are useful when calculated using imputed vital rates. I found that some missing vital rates, such as adult survival, could be imputed relatively accurately under a multivariate framework which accounted for covariance among rates of survival, reproduction, and maturation, even when phylogenetic information was not included. Accounting for phylogenetic relationships improved the accuracy of imputed values for vital rates with high phylogenetic signal (Pagel's $\lambda > 0.8$). However, including body mass and life history trait data also tended to improve imputation accuracy and to compensate for lack of phylogeny. Estimates of demographic metrics were sensitive to the accuracy of imputed vital rates.

In Chapter 4, I explored the use of life history indicators to assess vulnerability to mortality impacts in seabirds. This work addresses again the issue of incomplete data, but from the perspective of how hard it is to collect demographic data. Here I focus on whether there are easier metrics to collect that would be informative about population responses to disturbance. Life history theory tells us that long-lived species are more sensitive to mortality impacts than short-lived species, hence a metric that captures the fast-slow continuum of life history variation could be a useful proxy to capture population responses to excess mortality. If such a proxy can be derived from more readily available trait data this would be valuable for conservation assessment purposes when detailed demographic information is lacking (Stahl and Oli 2006). I investigated the use of two proxies of pace of life, generation time and the major axis of life history variation defined by a phylogenetic principal component analysis, as surrogate metrics for assessing the impact of mortality events on long- and short-term population growth. I found that the two pace of life indicators could be used as proxies for some demographic responses to elevated mortality risk in seabirds. The magnitude of elasticity of population growth rate to mortality hazard rate reduced as pace of life slowed. The sensitivity of transient amplification metrics to mortality hazard rate also tended to decrease for slower species and slower-paced species showed a tendency for slower recovery from impacts. While the strength of the relationships was relatively slight in some cases, pace of life indicators could be used in combination with other indicators (e.g. ecological or behavioural, Furness et al. 2013) to assess risk to seabirds from extrinsic threats, even when direct knowledge of demographic responses is lacking.

Finally, in Chapter 5, I carried out a literature review on demographic responses to climate in mammals to capture the current state of knowledge on mammalian species' responses to climate change. I did this as a primary contributor to the sAPROPOS climate and demography working group. This work again focused on the quality and availability of critical demographic data necessary to make inference and develop models for conservation. Specifically, the work focused on demographic responses to climatic drivers in mammals, one of the best-studied taxonomic groups, with the key objective to identify gaps in data for specific taxonomic groups. As a primary author, I contributed to planning and writing the manuscript, I helped to design and implement the literature review protocol and I developed and delivered key analyses for the final manuscript, including analyses exploring how demographic responses to climate in mammals align with vulnerability indicators and IUCN threat levels and whether complex demographic responses reflected IUCN assessed climate threat. Our results highlight key gaps in knowledge about how climate drivers influence vital rates of survival, development and reproduction in mammals. We found that data on demographic responses to climate are subject to extensive geographic and taxonomic biases and that demographic responses to climate are often complex. Critical gaps in demographic knowledge hinder a full understanding of mammal population responses to climate change.

6.2 Prospects for future work

There are several opportunities to advance the work presented here by incorporating additional features into the models to improve applicability or to explore related questions, by broadening the scope of the analyses and by developing case studies to demonstrate application of the techniques developed here.

In exploring the influence of pairing and divorce dynamics on population growth I made the assumption that divorce was costly only in terms of loss of reproductive output. Alternative divorce costs are possible. For example, individuals may be more likely to suffer mortality (Nicolai et al. 2012, Leach 2015), may have limited opportunities to find another mate because pairing opportunities are linked to age or experience (Black and Owen 1995, Cézilly et al. 1997, Jouventin et al. 1999), or may be less likely to find an experienced mate (Leach and Sedinger 2016). The framework developed here is robust and can accommodate these changes in assumptions, allowing an assessment of the relative effects of different forms of divorce on long- and short-term population growth in long-lived species. Developing the model to incorporate age- or experience-based pairing would require an extension of the pairing mechanism to include this aspect of individual state. The low sensitivity and elasticity of population growth rate to reproductive output in long-lived species that we observed in our analysis of this system suggests that, unless there is a strong link between pairing and divorce processes and survival, it is unlikely that these processes would have a large influence on population growth rate. Therefore pairing and divorce processes are unlikely to be of significant conservation concern unless divorce induces a high mortality risk, as may be the case for species with a social pair bond that is maintained through the annual lifecycle (Nicolai et al. 2012, Leach 2015).

In sexual populations, frequency-dependent mechanisms such as the availability of potential mates are influential on population dynamics (Rankin and Kokko 2007, Schindler et al. 2013, Haridas et al. 2014, Compagnoni et al. 2017). Understanding such mechanisms has relevance for conservation biology (Sæther et al. 2004, Gerber and White 2014), predicting responses to environmental change (Petry et al. 2016, Coulson et al. 2017), invasive species management (Miller et al. 2011, Erickson et al. 2017) and disease control (Taghikhani et al. 2020). In Chapter 2, I made the simplifying assumption of symmetric demography to allow investigation of the population-level consequences of individual quality-based pairing and divorce processes without having to disentangle the effects of frequency-dependence. However, sex-based differences in demography exist and can influence population dynamics and selection (Schindler et al. 2015, Gownaris and Boersma 2019, de Vries and Caswell 2019). For example, frequency dependence arising due to asymmetric demography influences the strength of the effect of pairing processes on population growth (Schindler et al. 2013). A model incorporating frequency dependence could be used to explore different questions such as considering the influence of a divorce rate which depends on the availability of opposite sex singletons (e.g. Maxin and Berec 2010) on population dynamics in structured populations. Frequency-dependent divorce and pairing are likely to have particular significance for smaller populations, where demographic stochasticity (that is, random variation in the fate of individuals) influences extinction risk (Legendre et al. 1999, Lee et al. 2011), so remains an important consideration for conservation management.

The assessment of the use of phylogenetic imputation analysis for imputing vital rates in Chapter 3 would have been complemented by an example use case to demonstrate the difference this method could make in assessing the conservation status of at-risk species. For example, almost a third of parrots are considered at risk according to IUCN Red List assessments (Handbook of the Birds of the World and BirdLife International 2019) but many parrot species lack accurate information on adult survival due to the challenges of marking individuals of these species. Demographic modelling of parrots is hindered by the lack of survival estimates, with *ad hoc* approaches commonly being used to substitute for missing values (Rodríguez et al. 2004, Koenig 2008). Applying phylogenetic imputation to estimate adult survival in large parrots would produce more robust estimates of population trajectories and more reliable analysis of population responses to perturbations, as well as informing estimates of key demographic metrics such as generation time. Furthermore, a suitably parameterised structured population model would allow estimation of stage distributions which could help to inform estimates of population abundance in species where juvenile and adult stages are not easily distinguished (Martin et al. 2020). Estimates of changes in abundance of mature individuals, in combination with estimates of generation time, which are used as a timescale over which to assess population trends, determine IUCN Red List status (IUCN Standards and Petitions Subcommittee 2019), so imputed survival data could play a critical role in assigning appropriate threat status to at-risk species. The small number of species in the baseline data set used for the imputation analysis hindered the development of such a case study. However, some of the data that was removed by the quality control process could, with appropriate correction, be used to augment the set of standardised vital rates used here, thereby providing a sounder basis for estimating vital rates for species of interest.

Imputing maturation rate for avian species was problematic due to the bimodal distribution of maturation rates which arises from life history variation among species with early and delayed maturation. Maturation rate was poorly handled under the distributional assumptions of the imputation model used in the analysis, which is conditioned on multivariate normal data. To account for the bimodal distribution of maturation rates an alternative model such as a two-component mixture model could be used. Mixture models represent the distribution of a random variable as a weighted composition of a number of component distributions and hence can be used to capture multimodal distributions. Mixture models have been applied to a variety of ecological and evolutionary phenomena (Martin et al. 2005, Podlaski and Roesch 2014, Hamel et al. 2017, Dupont et al. 2018). Assuming a given parametric form for the component distributions, expectation maximisation methods can be used to calculate maximum-likelihood estimates of the distributional parameters and their associated weights. The development of an imputation framework incorporating a mixture model for the estimation of maturation rates would be a potential improvement over the approach presented here.

A further extension of this work would be to use the outputs (imputed vital rates or estimated demographic metrics) as priors in a Bayesian analysis to produce credible intervals for the estimates. This would be valuable in applications such as assessment of extinction risk status, where decisions for categorising species under particular threat status are based on knowledge of demographic metrics such as generation time and have implications for conservation priority setting and action plans.

The comparative study of the use of proxies to predict seabird demographic responses to mortality in Chapter 4 was limited to seabird species which occur in UK waters. A broader analysis which incorporated a wider range of seabird species would determine whether the relationships between pace of life and sensitivities of long- and short-term population growth rate that were observed here are replicated across a wider set of species. It may also be instructive to consider other avian orders or other taxonomic groups. It would be appropriate in a wider study of avian species to control for latitudinal variation in life history traits such as clutch size (Jetz et al. 2008) and survival (Scholer et al. 2020), since these traits underlie the pace of life indicators. Here, I focused on using life history indicators to explore population responses to excess mortality, on the basis that survival is the vital rate with the greatest potential to produce changes in population growth rate in long-lived species. Comparison of the responses of population growth to other vital rates such as reproductive output may provide a useful indication of whether pace of life indicators also capture differences in population responses to perturbations of those vital rates.

A natural extension to the current study would be a case study incorporating pace of life indicators into an assessment of how seabird populations respond to mortality threats such as those caused by human disturbance of the marine environment. For example, ecology and behavioural metrics have been used to assess vulnerability of seabird populations to UK offshore energy infrastructure (Furness et al. 2012, 2013). In these assessments, species vulnerability is characterised as a metric based on mechanistic risk of mortality or disturbance determined by ecological and behavioural traits, modulated by a factor included as an indication of a species' "conservation importance". This multiplier may more accurately be considered as an *a priori* qualitative assessment of vulnerability, based on population trends, species range and life history in the form of adult survival rate (Furness et al. 2012). A pace of life indicator of population responses to additional mortality promises to provide a more robust quantitative basis for assessment of vulnerability of seabird species, potentially improving assignment of risk status on the basis of a more nuanced understanding of how life history influences individual species' responses to mortality.

6.3 Conclusions

Despite numerous advances in modelling approaches, the fundamental problem for conservation practitioners remains: how to prioritise conservation effort in the face of limited demographic data (Kindsvater et al. 2018, Conde et al. 2019) and limited budgets (Wilson et al. 2006), and how to communicate priorities to decision-makers and funders given these limitations and the uncertainty they generate (Milner-Gulland and Shea 2017). Conservation decision-making is often carried out without the opportunity for a high level of investment in acquiring new knowledge and must rely on existing data, so the development of techniques for making the best use of existing data and accounting for the uncertainties that arise due to data limitations remains a priority for conservation demography.

6.4 References

Black JM, Owen M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *The Journal of Animal Ecology*, **64**(2), 234.

Cézilly F, Boy V, Tourenq CJ, Johnson AR. 1997. Age-assortative pairing in the Greater Flamingo *Phoenicopterus ruber roseus*. *Ibis*, **139**(2), 331–336.

Compagnoni A, Steigman K, Miller TEX. 2017. Can't live with them, can't live without them? Balancing mating and competition in two-sex populations. *Proceedings of the Royal Society B: Biological Sciences*, **284**(1865), 20171999.

Conde DA, et al. 2019. Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences*, **116**(19), 9658–9664.

Coulson T, Kendall BE, Barthold J, Plard F, Schindler S, Ozgul A, Gaillard JM. 2017. Modeling adaptive and nonadaptive responses of populations to environmental change. *The American Naturalist*, **190**(3), 313–336.

de Vries C, Caswell H. 2019. Selection in two-sex stage-structured populations: genetics, demography, and polymorphism. *Theoretical Population Biology*, **130**, 160–169.

Dupont P, Allainé D, Cohas A, Pradel R. 2018. Testing determinants of the annual individual fitness: an overall mean mixture model for de-lifing data. *Methods in Ecology and Evolution*, **9**(3), 668–680.

Erickson RA, Eager EA, Brey MK, Hansen MJ, Kocovsky PM. 2017. An integral projection model with YY-males and application to evaluating grass carp control. *Ecological Modelling*, **361**, 14–25.

Furness RW, Wade HM, Masden EA. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, **119**, 56–66.

Furness RW, Wade HM, Robbins AMC, Masden EA. 2012. Assessing the sensitivity of seabird populations to adverse effects from tidal stream turbines and wave energy devices. *ICES Journal of Marine Science*, **69**(8), 1466–1479.

Gerber LR, White ER. 2014. Two-sex matrix models in assessing population viability: when do male dynamics matter? *Journal of Applied Ecology*, **51**(1), 270–278.

Gownaris NJ, Boersma PD. 2019. Sex-biased survival contributes to population decline in a long-lived seabird, the Magellanic Penguin. *Ecological Applications*, **29**(1), e01826.

Hamel S, Yoccoz NG, Gaillard JM. 2017. Assessing variation in life-history tactics within a population using mixture regression models: a practical guide for evolutionary ecologists. *Biological Reviews*, **92**(2), 754–775.

Handbook of the Birds of the World and BirdLife International. 2019. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world: Version 4 (December 2019). Available at: http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v4_Dec19.zip (accessed September 2020).

Haridas CV, Eager EA, Rebarber R, Tenhumberg B. 2014. Frequency-dependent population dynamics: effect of sex ratio and mating system on the elasticity of population growth rate. *Theoretical Population Biology*, **97**, 49–56.

IUCN Standards and Petitions Subcommittee. 2019. Guidelines for using the IUCN Red List categories and criteria. Tech. Rep. Version 14, prepared by the Standards and Petitions Subcommittee. Available from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed November 2019).

Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch size across species and space. *PLOS Biology*, **6**(12), e303.

Jouventin P, Lequette B, Dobson FS. 1999. Age-related mate choice in the wandering albatross. *Animal Behaviour*, **57**(5), 1099–1106.

Kindsvater HK, Dulvy NK, Horswill C, Juan-Jordá MJ, Mangel M, Matthiopoulos J. 2018. Overcoming the data crisis in biodiversity conservation. *Trends in Ecology & Evolution*, **33**(9), 676–688.

Koenig SE. 2008. Black-billed Parrot (*Amazona agilis*) population viability assessment (PVA): a science-based prediction for policy makers. *Ornitología Neotropical*, **19**, 135–149.

Leach A. 2015. *Fitness Consequences of Clutch Size Decisions and Mate Change in Black Brant*. Ph.D. thesis, University of Nevada, Reno.

Leach AG, Sedinger JS. 2016. Male breeding experience, not mate familiarity, affects reproductive output in black brant geese. *Behavioral Ecology*, **27**(6), 1851–1858.

Lee AM, Sæther BE, Engen S, Eckert AECG, McPeek EMA. 2011. Demographic stochasticity, Allee effects, and extinction: the influence of mating system and sex ratio. *The American Naturalist*, **177**(3), 301–313.

Legendre S, Clobert J, Møller AP, Sorci G, Gotelli AENJ, Harrison S. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *The American Naturalist*, **153**(5), 449–463.

Martin R, Haines J, Gilardi JD. 2020. Assessing population trends in a threatened parrot using a long-term community-based roost monitoring programme. Manuscript in preparation.

Martin TG, Kuhnert PM, Mengersen K, Possingham HP. 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications*, **15**(1), 266–280.

Maxin D, Berec L. 2010. A two-sex demographic model with single-dependent divorce rate. *Journal of Theoretical Biology*, **265**(4), 647–656.

Miller TEX, Shaw AK, Inouye BD, Neubert MG, Bolker AEBM, McPeek EMA. 2011. Sex-biased dispersal and the speed of two-sex invasions. *The American Naturalist*, **177**(5), 549–561.

Milner-Gulland EJ, Shea K. 2017. Embracing uncertainty in applied ecology. *Journal of Applied Ecology*, **54**(6), 2063–2068.

Nicolai CA, Sedinger JS, Ward DH, Boyd WS. 2012. Mate loss affects survival but not breeding in black brant geese. *Behavioral Ecology*, **23**(3), 643–648.

Petry WK, Soule JD, Iler AM, Chicas-Mosier A, Inouye DW, Miller TEX, Mooney KA. 2016. Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science*, **353**(6294), 69–71.

Podlaski R, Roesch FA. 2014. Modelling diameter distributions of two-cohort forest stands with various proportions of dominant species: A two-component mixture model approach. *Mathematical Biosciences*, **249**, 60–74.

Rankin DJ, Kokko H. 2007. Do males matter? The role of males in population dynamics. *Oikos*, **116**(2), 335–348.

Rodríguez J, Fajardo L, Herrera I, Sánchez A, Reyes A. 2004. Yellow-shouldered Parrot (*Amazona barbadensis*) on the islands of Margarita and La Blanquilla, Venezuela. In Akçakaya HR, Burgman MA, Kindvall O, Wood CC, Sjogren-Gulve P, Hatfield JS, McCarthy MA, eds., *Species conservation and management: case studies*, pp. 361–370. Oxford University Press, Oxford.

Sæther BE, Engen S, Lande R, Møller AP, Bensch S, Hasselquist D, Beier J, Leisler B. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. *Journal of Animal Ecology*, **73**(5), 925–934.

Schindler S, Gaillard JM, Grüning A, Neuhaus P, Traill LW, Tuljapurkar S, Coulson T. 2015. Sex-specific demography and generalization of the Trivers-Willard theory. *Nature*, **526**(7572), 249–252.

Schindler S, Neuhaus P, Gaillard JM, Coulson T. 2013. The influence of nonrandom mating on population growth. *The American Naturalist*, **182**(1), 28–41.

Scholer MN, Strimas-Mackey M, Jankowski JE. 2020. A meta-analysis of global avian survival across species and latitude. *Ecology Letters*, **23**(10), 1537–1549.

Stahl JT, Oli MK. 2006. Relative importance of avian life-history variables to population growth rate. *Ecological Modelling*, **198**(1–2), 23–39.

Taghikhani R, Sharomi O, Gumel AB. 2020. Dynamics of a two-sex model for the population ecology of dengue mosquitoes in the presence of Wolbachia. *Mathematical Biosciences*, **328**, 108426.

Wilson KA, McBride MF, Bode M, Possingham HP. 2006. Prioritizing global conservation efforts. *Nature*, **440**(7082), 337–340.