

Bridging gaps in demographic analysis using phylogenetic imputation

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 such 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 of focal species 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 model parameters, awareness of the sensitivities of demographic model outputs to the imputed vital rates is essential.

29 **Introduction**

30 Globally, biodiversity faces an unprecedented threat of extinction (Barnosky et al. 2011;
31 Pimm et al. 2014; Ceballos et al. 2015), driven by human-induced threats such as habitat
32 loss and degradation, climate change, and overexploitation (Brook et al. 2003; Parmesan
33 2006; Maclean & Wilson 2011; Maxwell et al. 2016). Understanding population responses
34 to such threats is crucial for identifying at-risk species and to guide conservation
35 interventions (e.g. Bruna et al. 2009; Dahlgren et al. 2016; Lunn et al. 2016). Population
36 models parameterized with estimates of vital rates of survival, development, and
37 reproduction can be used to generate predictions about how a population will respond to
38 pressures that cause changes to vital rates (Selwood et al. 2015).

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

48 When data are missing for a focal species, *ad hoc* imputation methods are commonly
49 used to fill in such gaps for demographic modelling (Beissinger & Westphal 1998).
50 Parameter estimates may be derived from empirical data for other species based on
51 relatedness (Heinsohn et al. 2004; Koenig 2008) or trait similarity (McCarthy et al. 1999;
52 Valle et al. 2018). Other approaches include combining estimates from populations to form
53 a representative model for a species (Sæther & Bakke, 2000), or parameterization of models
54 based on a range of plausible values (Rodríguez et al. 2004) or on data from captive
55 individuals (e.g. Young et al. 2012). Such approaches produce bias (Schafer & Graham 2002)

56 and their use raises concerns about the reliability of model outputs and the ability to make
57 robust conclusions (Sæther & Engen, 2002; Ellner & Fieberg, 2003; McGowan et al. 2011).
58 Therefore, formal methods for estimating missing vital rates and quantifying uncertainty in
59 such estimates are needed.

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

73 Phylogenetic imputation has been proposed for filling gaps in functional trait data in
74 plants (Swenson 2014) and mammals (Guénard et al. 2013; Penone et al. 2014). Such
75 methods have rarely been applied to demographic data, although hierarchical approaches
76 incorporating taxonomy have been used to estimate life history parameters in fish (Thorson
77 et al 2017). Here, we focus on demographic traits, namely vital rates of survival, maturation
78 and fecundity. In plants, imputation of single vital rates suggested that neither fecundity nor
79 the survival of different life stages were strongly predicted by phylogeny or species-level
80 traits (Che-Castaldo et al. 2018), reflecting weak phylogenetic signal in plant vital rates
81 (Burns et al. 2010). In vertebrates, strong phylogenetic signal in characteristics that covary
82 with vital rates (body size, morphology and life history traits) has been interpreted as being
83 informative about evolutionary processes such as the strength of stabilising selection and

84 evolutionary lability (Blomberg et al. 2003; but see Revell et al. 2008). Whatever the exact
85 evolutionary processes involved, the tendency of vital rates to covary with body size
86 (Stearns 1983) and life history traits (e.g. age at maturity and clutch size, Sæther & Bakke
87 2000) suggests that they will also have strong phylogenetic signal, which would be useful in
88 an applied setting to infer vital rates for related species. The inclusion of covarying
89 allometric and life history trait data may help to inform the imputation of vital rates (e.g.
90 Shine & Charnov 1992; Brawn et al. 1995).

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

107 Here, we use existing vital rate data for birds to assess the feasibility of using
108 phylogenetic imputation to fill gaps in demographic analysis. While much avian
109 demographic data has been compiled (Sæther & Bakke 2000; Lebreton et al. 2012; Salguero-
110 Gómez et al. 2016), information about vital rates is missing for many species of conservation
111 concern (e.g. survival is missing for 82% of bird species, Conde et al. 2019). We use

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.

Methods

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

Standardized vital rate, body mass and life history trait data

We extracted matrix population models for birds from the COMADRE Animal Matrix Database (version 3.0.1, COMADRE 2019) and other sources (Sæther & 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 (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 & 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 & 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 (Supporting Information). We combined the standardized vital rates with avian body mass, clutch size, and female age at maturity (Wilman et al. 2014; Myhrvold et al. 2015) and transformed all variables to satisfy the requirements of the imputation model (Supporting Information).

Phylogeny

We downloaded a sample of 1,000 full avian phylogenetic trees (Hackett backbone) 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 (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 (Supporting Information).

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 among 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 1,000 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.

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. 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. 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. 1). Within each trait dataset, we introduced a known structure of missing values among the vital rates for a focal species. We removed vital rate values in all possible combinations of single and multiple vital rates, resulting in 15 datasets per species (Missing data combinations, Fig. 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),

$$\text{NRMSE} = \frac{\sqrt{\frac{\sum_i (X_i^* - X_i)^2}{n}}}{\max_i(X_i) - \min_i(X_i)}, \quad (1)$$

to assess imputation accuracy for each vital rate, missing vital rate combination and trait dataset. Here, X_i^* and X_i represent imputed and original values, respectively, of a vital rate for species i . Normalization 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 (Supporting Information).

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,

$$\mathbf{A} = \begin{bmatrix} s_0 f & s_a f \\ s_0 & s_a \end{bmatrix}, \quad (2)$$

and for delayed maturation species,

$$\mathbf{A} = \begin{bmatrix} 0 & m s_a f & s_a f \\ s_0 & (1 - m) s_a & 0 \\ 0 & m s_a & s_a \end{bmatrix}. \quad (3)$$

We used these population models to generate population growth and life history metrics (Table 1). For each missing data combination and trait dataset, we calculated the normalized root mean square error (Equation 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.

Results

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 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 further improvement and may even act slightly negatively on phylogenetic signal.

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. 2). However, phylogenetic information helped to improve imputation 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. 2) and reduced the difference in accuracy between phylogenetic and null models for adult survival.

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), despite differences in imputation accuracy for these vital rates (Fig. 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 (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). 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 (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.

Population growth metrics

Population growth rate

When maturation rate was imputed, population growth rates matched the original values reasonably well (mean NRMSE: 0.051, SD <0.001, Fig. 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 (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. 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 elasticities were unbiased except when maturation rate was imputed (Supporting Information).

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 extinction risk (Fung & 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 (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 & Diaz-Lopez 2017). Many studies have advised caution in

the interpretation of demographic model outputs due to parameter uncertainty (Beissinger & 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 & 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 & 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).

Supporting Information

Data extraction procedure, species list, phylogenetic tree, and taxonomic bias (Appendices S1–S4); exploration of phylogenetic uncertainty (Appendix S5); comparison of imputation with and without phenotypic variation (Appendix S6); observed vs imputed vital rates for post-breeding census data under the null (Appendices S7–S10) and phylogenetic (Appendices S11–S14) models; observed vs imputed vital rates for pre-breeding census data under the null and phylogenetic models (Appendices S15–S16); and results for life history (Appendices S17–S19) and population growth (Appendices S20–S22) 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.

Literature Cited

- 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. *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):1–8.
- 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*. DOI: 10.1111/cobi.13486.
- 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.

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

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

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

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

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

398 Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated
399 modern human-induced species losses: Entering the sixth mass extinction. *Science*
400 *Advances*, **1**(5):e1400253. DOI: 10.1126/sciadv.1400253.

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

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

404 COMADRE. 2019. COMADRE Animal Matrix Database (v.3.0.1). Available from
405 <https://www.compadre-db.org> (accessed April 2020).

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

408 Cooke RSC, Gilbert TC, Riordan P, Mallon D. 2018. Improving generation length estimates
409 for the IUCN Red List. PLOS ONE **13**(1):e0191770. DOI: 10.1371/journal.pone.0191770.

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

412 Dahlgren DK, Guttery MR, Messmer TA, Caudill D, Dwayne Elmore R, Chi R, Koons DN.
413 2016. Evaluating vital rate contributions to greater sage-grouse population dynamics to
414 inform conservation. Ecosphere. **7**(3):e01249. DOI: 10.1002/ecs2.1249.

415 dos Santos JW, Correia RA, Malhado ACM, Campos-Silva JV, Teles D, Jepson P, Ladle RJ.
416 2020. Drivers of taxonomic bias in conservation research: a global analysis of terrestrial
417 mammals. Animal Conservation. DOI: 10.1111/acv.12586.

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

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

422 Fagan WF, Pearson YE, Larsen EA, Lynch HJ, Turner JB, Staver H, Noble AE, Bewick S,
423 Goldberg EE. 2013. Phylogenetic prediction of the maximum per capita rate of
424 population growth. Proceedings of the Royal Society B: Biological Sciences
425 **280**(1763):20130523.

426 Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist
427 **125**(1):1–15.

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

430 Fujiwara M, Diaz-Lopez J. 2017. Constructing stage-structured matrix population models
431 from life tables: comparison of methods. PeerJ **5**:e3971. DOI: 10.7717/peerj.3971.

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

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

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

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

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

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

447 Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch
 448 size across species and space. PLOS Biology **6**(12):e303. DOI:
 449 10.1371/journal.pbio.0060303.

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

452 Kendall BE, Fujiwara M, Diaz-Lopez J, Schneider S, Voigt J, Wiesner S. 2019. Persistent
 453 problems in the construction of matrix population models. Ecological Modelling
 454 **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. *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.

480 McCarthy MA, Webster A, Loyn RH, Lowe KW. 1999. Uncertainty in assessing the viability
 481 of the Powerful Owl *Ninox strenua* in Victoria, Australia. *Pacific Conservation Biology*
 482 **5**(2):144–154.

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

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

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

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

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

494 Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature*
 495 **401**(6756):877–884.

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

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

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

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

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

508 Reed JM, Mills LS, Dunning JB, Menges ES, McKelvey KS, Frye R, Beissinger SR, Anstett MC,
509 Miller P. 2002. Emerging issues in population viability analysis. *Conservation Biology*
510 **16**(1):7–19.

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

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

515 Roberts BEI, Harris WE, Hilton GM, Marsden SJ. 2016. Taxonomic and geographic bias in
516 conservation biology research: a systematic review of wildfowl demography studies.
517 *PLOS ONE* **11**(5):e0153908. DOI: 10.1371/journal.pone.0153908.

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

520 Rodríguez J, Fajardo L, Herrera I, Sánchez A, Reyes A. 2004. Yellow-shouldered Parrot
521 (*Amazona barbadensis*) on the islands of Margarita and La Blanquilla, Venezuela. Pages
522 361–370 in Akçakaya HR, et al., editors. *Species conservation and management: case*
523 *studies*. Oxford University Press, Oxford.

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

526 Sæther BE, Engen S. 2002. Pattern of variation in avian population growth rates.
 527 Philosophical Transactions of the Royal Society B: Biological Sciences **357**(1425):1185–
 528 1195.

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

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

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

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

537 Scholer MN, Strimas-Mackey M, Jankowski JE. 2020. A meta-analysis of global avian
 538 survival across species and latitude. Ecology Letters. Advance online publication. DOI:
 539 10.1111/ele.13573.

540 Selwood KE, McGeoch MA, Mac Nally R. 2015. The effects of climate change and land-use
 541 change on demographic rates and population viability. Biological Reviews **90**(3):837–
 542 853.

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

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

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

550 Swenson NG. 2014. Phylogenetic imputation of plant functional trait databases. *Ecography*
551 **37**(2):105–110.

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

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

556 Valle S, Collar NJ, Harris WE, Marsden SJ. 2018. Trapping method and quota observance
557 are pivotal to population stability in a harvested parrot. *Biological Conservation*
558 **217**:428–436.

559 Weimerskirch H. 2001. Seabird demography and its relationship with the marine
560 environment. Pages 115–135 in Schreiber EA, Burger J, editors. *Biology of marine birds*.
561 CRC Press, Boca Raton, Florida.

562 Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014. Elton-Traits
563 1.0: species-level foraging attributes of the world’s birds and mammals. *Ecology*
564 **95**(7):2027–2027.

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

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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

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Table 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.

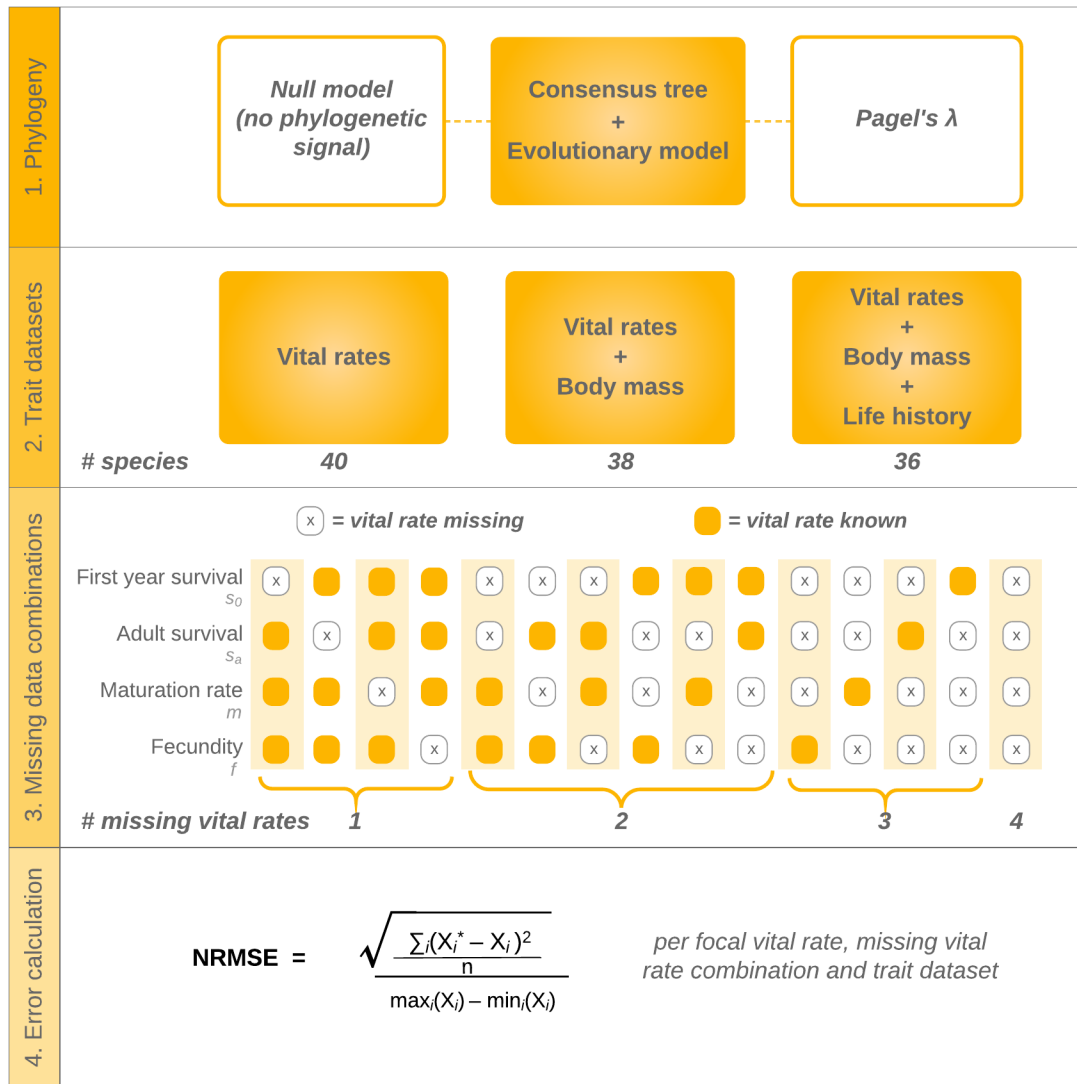
Figure 1: We applied phylogenetic imputation to vital rate, body mass and life history trait data to assess the accuracy of predicting vital rates for use in demographic models. Our key questions related to phylogeny, trait data, and missing data structure. 1. Does including phylogenetic relationships 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.

Figure 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.

Figure 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

597 metric estimate are not shown. Filled symbols show the mean errors across trait datasets
598 and open symbols show errors for individual trait datasets.

599 Figure 4: Estimates of population growth rate (a) and sensitivity and elasticity of population
600 growth rate to underlying vital rates (b) varied in accuracy when vital rates were imputed,
601 with imputed fecundity causing the least accurate values in many cases. Accuracy was
602 similar across trait datasets except in two cases when life history trait data reduced the
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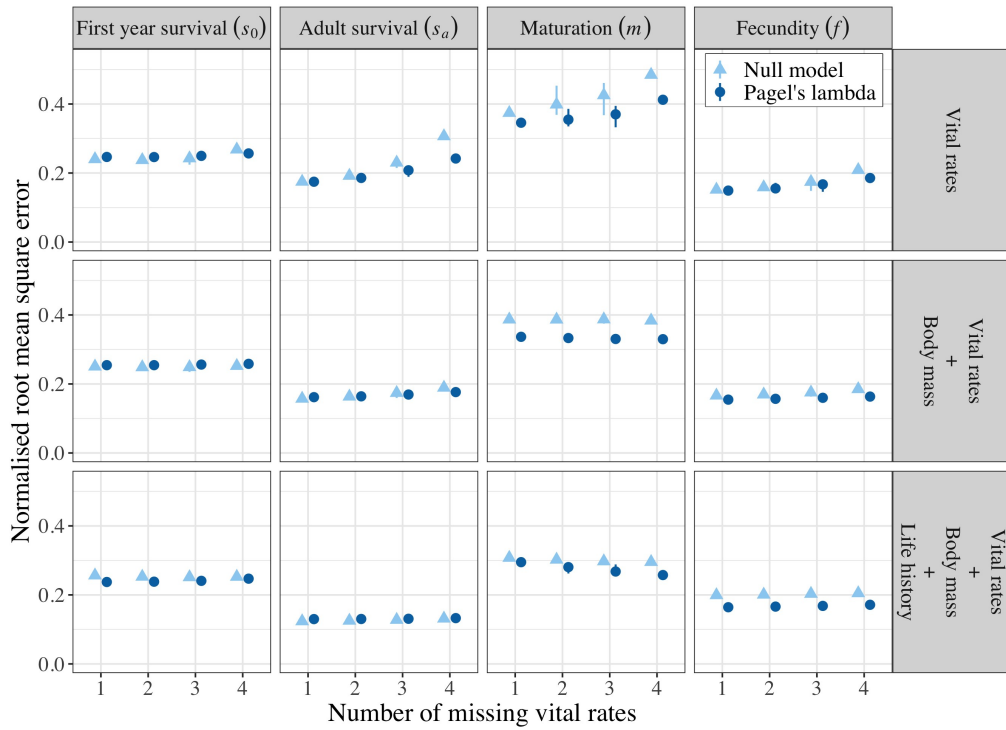
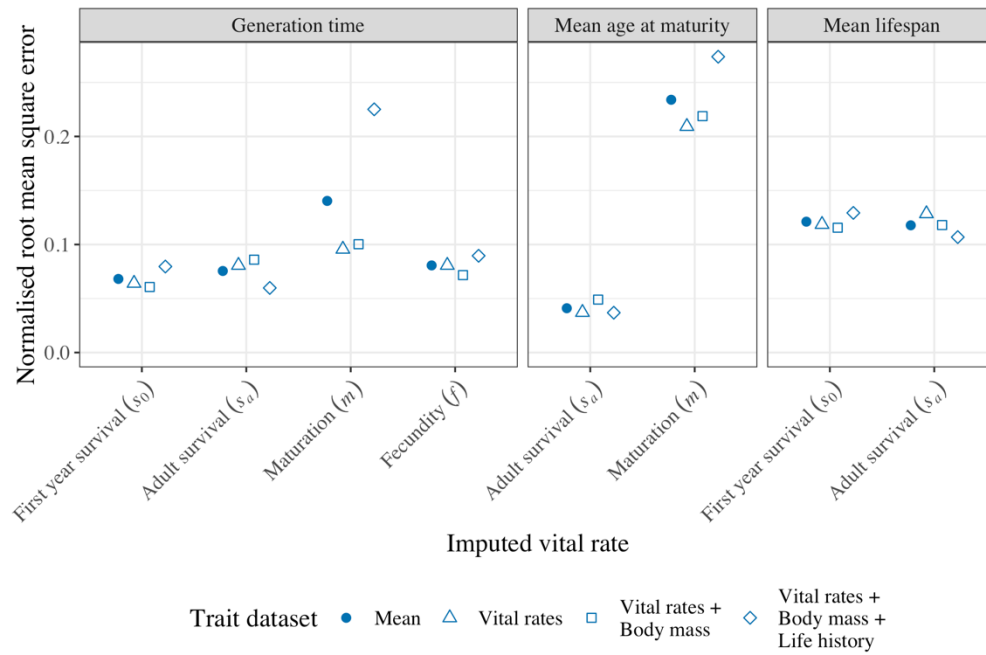


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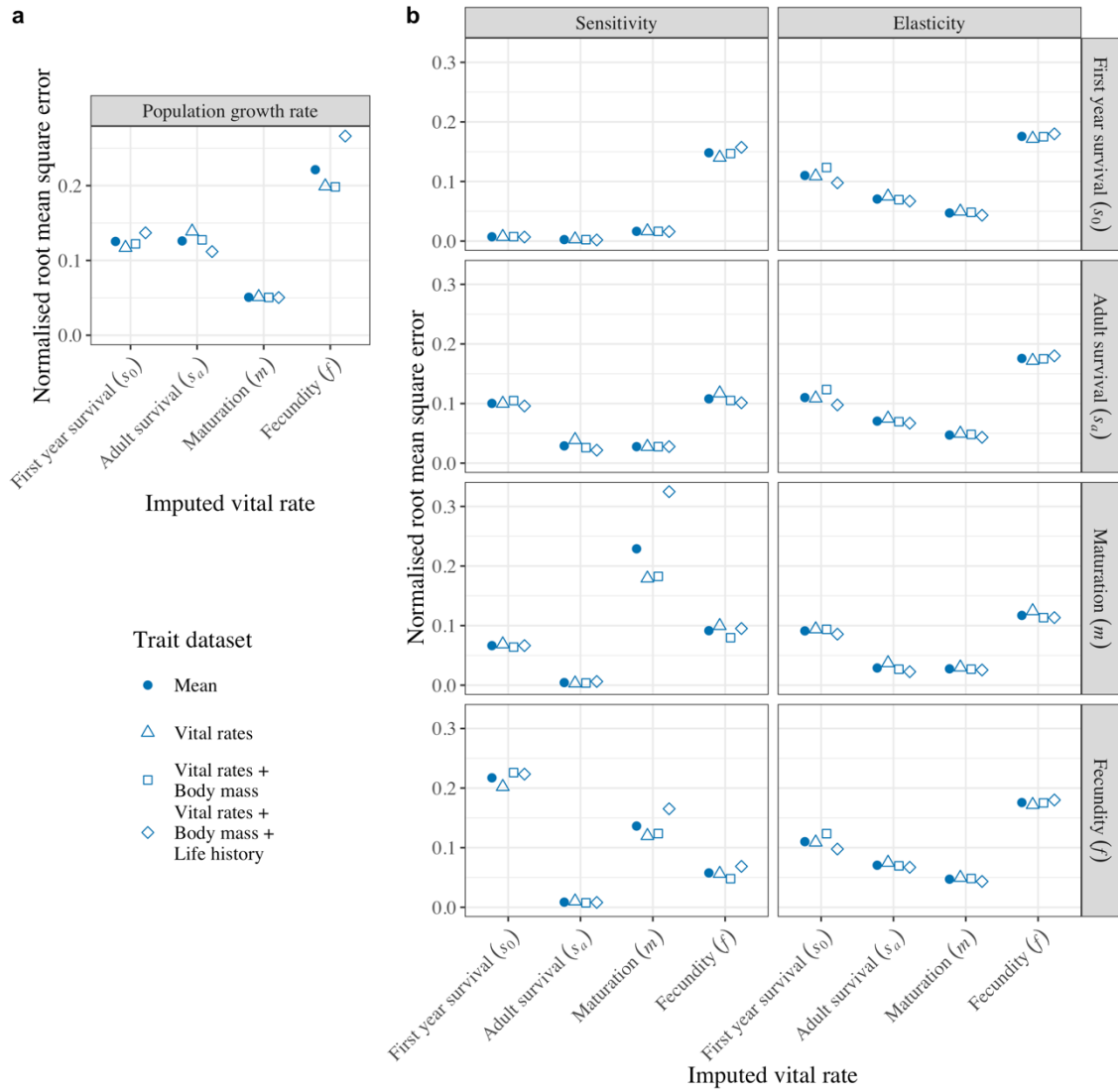


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