Generation lengths of the world's birds and their implications for extinction risk

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Article impact statement

Accurate generation lengths for all birds will improve assessment of extinction within the group.

Abstract

Birds have been comprehensively assessed on the IUCN Red List more times than any other taxonomic group. However, to date, generation lengths have not been systematically estimated to scale population trends when undertaking assessments, as required by the Red List Criteria. We compiled information from major databases of published life history and trait data for all birds, and imputed missing life history data as a function of species traits using Generalized Linear Mixed Models. Generation lengths were derived for all species, based on our modelled values of age-at-first-breeding (F), maximum longevity (L) and annual adult survival (S). The resulting generation lengths vary from 1.42 to 27.87 years, with a median of 2.99 years. We found that most species (61%) have generation lengths shorter than 3.33 years, meaning that the period of three generations - over which population declines are assessed under Criterion A of the Red List - was shorter than 10 years, the value used for Red List assessments of species with short generation times. For these species, our trait-informed estimates of generation length suggest that 10 years is a robust precautionary value for threat assessment. In other cases, however, for whole families, genera or individual species, generation length has a substantial impact on their estimated extinction risk, resulting in higher extinction risk in longer-lived species. While our approach is an effective means of addressing data gaps, there is some evidence that generation lengths for some species may still have been underestimated, owing to a paucity of life history data. Overall, our results will strengthen future extinction risk assessments and augment key databases of avian life history and trait data. We hope the findings stimulate future research to fill the remaining data gaps.

Introduction

Species' generation lengths, defined as "the average age of parents of the current cohort" (IUCN 2019), have been applied broadly within ecology as a metric of life-history variation (Gaillard et al. 2005), when evaluating responses to variable environments (Tuljapurkar et al. 2009) and for calculating rates of evolution (Martin & Palumbi 1993; Evans et al. 2012). In conservation science,

generation lengths have been used as a proxy for climate-change adaptability in species (Pearson et al. 2014; Bay et al. 2018; Foden et al. 2019), incorporated into assessments of sustainability of bycatch (Dillingham 2010) and utilised for scaling population declines when measuring extinction risk (Mace et al. 2008). Calculating generation length requires age- and sex-specific information on survival and fecundity, best calculated from a 'life table' (IUCN 2019) or by using proxies based on age of first reproduction (F), maximum longevity (L) and annual adult survival (S) (Fung & Waples 2017; IUCN 2019). However, collection and publication of age-based vital-rate information peaked in the 1980s (Fung & Waples 2017), and reporting of life-history data such as F, L and S is also likely to be declining in birds, with recovery rates of marked individuals falling (Robinson et al. 2009). Attempts to calculate generation lengths are therefore often hampered by a lack of appropriate life history data, but approaches exist for extrapolating or imputing F, L and S from data for other species (Di Marco et al. 2012; Pacifici et al. 2013; Cooke et al. 2018).

Birds are among the best-studied taxa (Titley et al. 2017), yet to date generation lengths have not been systematically estimated for all species across the group. The conservation status of birds has been more thoroughly assessed than that of any other taxonomic group (BirdLife International 2018a). They were the first class to be comprehensively assessed on the IUCN (International Union for Conservation of Nature) Red List of Threatened Species (hereafter the Red List; Collar & Andrew 1988), the most widely adopted tool for assessing species' vulnerability to extinction (Mace et al. 2008). Birds have subsequently been comprehensively reassessed for the Red List six times (no other group has been assessed more than twice). Status assessments of birds have been central to highlighting the world's most threatened species, identifying impacts, directing conservation actions and charting trends in biodiversity (BirdLife International 2018a). Given this prominence, work is ongoing to improve estimates of the parameters underlying the Red List assessments for birds, of which generation length is important.

The Red List assigns species to categories of relative extinction risk using quantitative criteria based on their population sizes, trends and distribution (IUCN 2012). Rapid rates of population decline are associated with elevated extinction risk when scaled by generation length (O'Grady et al. 2008). This

scaling accounts for varying life history strategies and is used when assessing population declines on the Red List. This is particularly important under Red List Criterion A, which considers declines over 10 years or three generations, whichever is longer, and Criterion C, which considers population size, structure and trends scaled by generation length (IUCN 2012). As generation lengths have hitherto not been estimated systematically and consistently for all bird species on the Red List, we use available data to estimate F, L and S for all birds, and from these parameters we derive estimates of generation lengths. We then assess the implications for the Red List, in terms of the number of species qualifying within each category, when trends are scaled over three generations using our new estimates. Finally, we consider the broader implications of our results.

Methods

Data collation and modelling

We compiled a dataset of published values for F, L and S from a variety of sources (see Appendix S1). We compared two approaches for assigning values to species lacking a published estimate. First, we used a hierarchical extrapolation approach. We calculated genus, family and order means of F, L and S from published values and followed a taxonomic hierarchy to extrapolate missing values: when a species lacked a published estimate, but published estimates existed for one or more congener(s), the median of those values was assigned; when there were no published estimates for the entire genus, the mean of other values for the family were used; and when there were no published estimates for the entire family, the mean of other values for the order were used (Appendix S2). To test the strength of this approach, we compared each (i) published (P) value of F, L and S with predicted genus, family and order means recalculated without Pi. We calculated R^2 between the published and predicted values.

Second, we used a modelling approach. F, L and S are known to be correlated with a range of species traits, including body size and constraints associated with the environments that species inhabit

(Partridge & Harvey 1988; Sæther & Bakke 2000). We used selected avian species traits (Appendix S3) to model variation in F, L and S as a function of species traits, and used the resulting models to generate predicted F, L and S values for species that lacked published values, but where trait data were available. To do this, we fitted Generalized Linear Mixed Models (GLMMs) with nested random effects for order, family and genus to account for phylogenetic correlations, and body mass (log-transformed), migratory status, environmental associations (marine, freshwater or terrestrial) and diet as fixed effects for each of the three response parameters. We also included breeding range centroid latitudes (as absolute values, derived from BirdLife's global species distribution maps) as a fixed effect to account for tropical species often having slower life histories (Wiersma et al. 2007), and mean clutch size for a subset of species where estimates were available (N=2156 of 2401 species with data on F, L and/or S). We centred and standardized all continuous predictors prior to analysis and used a version of Akaike information criterion (AICc) to compare all possible fixed-effect combinations of the global model and select the best model for each response parameter (Table 1). In cases where multiple models were within 2ΔAIC$_c$ of the top-ranked model, we selected the model with the fewest parameters following the principle of parsimony (Arnold 2010). For S, we applied a logit transformation to normalize the response, while F and L were log-transformed and modelled as Gaussian responses (Quinn & Keough 2002). All models were fitted in R statistics version 3.3.1 using package 'lme4' (Bates et al. 2015). We checked residual diagnostic plots to determine data conformity to model assumptions, and used conditional and marginal R^2 values to evaluate the explanatory power of the best models (Fig. 1), calculated using methods described in Nakagawa & Schielzeth (2013). Having confirmed that the models performed adequately in explaining observed variation in F, L and S across species in the dataset (Table 2), we used the best models to predict values F, L and S for all species where relevant trait data were available. Complete data for all traits listed above were available for 9,484 species worldwide (Appendix S3), with the exception of clutch size, which was missing for 3,386 of those species. For species lacking clutch size data, we used the best model from a candidate set excluding clutch size to derive predicted values of F, L and S. For the remaining 1,642 species lacking data on two or more necessary traits for model prediction, we

assigned values of F, L and S using the means of other species in that genus, family or order, depending on availability (i.e. hierarchical extrapolation).

Having calculated the coefficient of determination between 1) published and extrapolated, and 2) published and modelled values of F, L and S, we compared the R^2 statistics to determine which approach generated values that best fitted the published data (Fig. 1).

Calculating generation lengths

We used the model-predicted values of F, L and S (Appendix S2) to estimate generation length in two ways: generation length based on F, L, and S ($G_{FLS;}$ equation 1) and generation length based on F and L (G_{FL}; equation 2).

$$G_{FLS} = \sum_{x=F}^{L} x l_x \bigg/ \sum_{x=F}^{L} l_x \qquad \text{(Eq. 1)}$$

where x is age in years, and the summations are from age (x) of first reproduction (F) to maximum longevity (L); and l_x is survivorship up to age x (i.e. $l_x = S_0 \cdot S_1 \cdots S_{x-1}$ where S is annual survival rate, and $l_0 = 1$ by definition; IUCN, 2019). Here we assumed $l_x = S^x$ (see below).

$$G_{FL} = F + z(L - F) \qquad \text{(Eq. 2)}$$

where z is a number between 0 and 1 (IUCN 2019). To calculate z, we first used Equation 1 for species with published values of F, L, and S. From these, we excluded species with $S < 0.3$ or $S^L < 10^{-5}$ because S is very likely underestimated for these species (see Discussion). This left 550 species, for which we calculated z using Equation 3:

$$z = (G_{FLS} - F_{\max})/(L_{\max} - F_{\max}) \qquad \text{(Eq. 3)}$$

where F_{max} and L_{max} are, for each species, the maximum of either the observed value or the modelled value. We calculated the average value of z for 4 groups (see Table 3), based on published F, and used these average values in Equation 2 to calculate G_{FL} for all species.

Equation 1 is simplified from the definition of G as the average age of parents (item 1 in IUCN 2019, section 4.4) to accommodate lack of age-specific survival and fecundity (m) values. It assumes that fecundity is zero for ages $<F$ and $>L$, and that annual rates of fecundity and survival do not change with age from age F to age L. As a result, Equation 1 does not include m, because it can be taken out of summation in both numerator and denominator and thus cancelled. We also assumed that annual survival rate from birth to age F (which does not change the calculation of G) is also S, resulting in the simplification $l_x = S^x$. Because Equation 1 can underestimate generation length under certain conditions (see Discussion), and because this may also affect the calculation of z (as Eq. 3 uses G_{FLS}), we defined generation length of each species as the larger of the two estimates (Appendix S4):

$$G = \max(G_{FLS}, G_{FL}) \qquad \text{(Eq. 4)}$$

For each species, we also calculated the difference between the two estimates, $G_{FL}–G_{FLS}$, and S^L, which is an estimate of the proportion of individuals reaching age L (see Discussion).

The definition of age is important for this calculation. We assume that the data sources we used are likely to define age such that an individual starting to breed (nesting, mating) at <12 months of age, in the breeding season after the one in which it fledged, is called one-year old, which is different from the definition used in the Red List Guidelines (IUCN 2019) and the workbook accompanying the guidelines. Therefore, we adjusted our methods to account for this difference.

An alternative formula for generation length is $G_{FS} = F+1/(1–S)$ (IUCN 2019), or $F+1/(1–S) –1$ with the definition of age used here. This formulation (also known as the adult mortality proxy) assumes that there is no senescence (i.e. survival and fecundity remain constant after age F), and therefore does

not use the information on maximum longevity. Therefore $G_{FS} > G_{FLS}$ for all species. We did not use G_{FS} because it would be a better estimate only for species for which S is relatively well known and L is unknown or underestimated—we do not believe this is the case for most bird species. In addition, the single value of S often available for all adult age classes means that G_{FS} ignores senescence; this is partially corrected by limiting the calculation of G_{FLS} (Eq. 1) to a maximum age of L.

Assessing Red List implications

We used the current population trend estimates from BirdLife International's Red List assessments (BirdLife International 2018b) to estimate species trends over both 10 years and three generations (Appendix S5). These trend estimates represent a percentage population decline/increase over a period of 10 years or three generations, whichever is longer, with the latter based on estimates of generation time based on earlier, incomplete, extrapolations from known parameter values from a smaller number of species. Most trend estimates are in bands representing uncertainty around precise values (e.g. 30-49% decline suspected over three generations) as they are based on sparse data, inference and expert opinion. In these cases, the true trend is believed to fall somewhere within the range, with plausible minimum and maximum values defined by the upper and lower limits of the banded range. We used 3 × the current generation time on the Red List assessment as an initial trend period (T_i). Minimum, median and maximum estimated trends were then extrapolated from T_i to $T_1 = 10$ years, and $T_2 = \max(10 \text{ years}, 3G)$, whichever is longer, as stipulated in the Red List Criteria (IUCN 2012). Minimum and maximum trend estimates were derived as follows: for all species recorded as currently declining, quantified trends were used if available (which was true for most threatened and Near Threatened species). For species with a currently declining trend but that lack a quantified trend estimate, a minimum decline of 1% and maximum of 24% was inferred, on the basis that none of these species are listed as threatened or Near Threatened under Criterion A (Appendix S5), while species with a rate of decline of ≥25% over 10 years or three generations are candidates for Near Threatened or threatened status (IUCN 2019). Median estimates were calculated as the mid-point of

the minimum and the maximum (if only a single value rather than a range was documented for the rate of decline in the Red List assessment for a particular species, this value was used for the minimum, median and maximum). We used both linear and exponential rates of change (IUCN 2019) to extrapolate trends, thereby generating two values for each minimum, median and maximum trend estimate for each species. Each species was given an overall minimum, median and maximum, using the highest of the respective values.

We compared the resultant trends against the thresholds for Red List Criteria A2-A4: >80% decline = Critically Endangered, 50-79% decline = Endangered, 30-49% decline = Vulnerable (IUCN 2012), and a derived threshold of 25-29% decline = Near Threatened. We quantified the number of species qualifying in threatened and Near Threatened categories under Criterion A for the different scenarios, and the number qualifying as threatened or Near Threatened overall when all Red List Criteria are applied.

Results

Estimating F, L and S

As with other taxa, information on F, L and S was lacking for most birds. We found published estimates for just 13.1%, 18.0% and 8.4% of the world's 11,126 extant bird species respectively (Appendix S1). Hierarchical extrapolation allowed us to generate missing values of F for 11,093 (99.7%), L for 11,097 (99.8%) and S for 10,936 (98.3%) of all species (Appendix S2). However, extrapolated values were poorer at predicting published estimates than were modelled values (Fig. 1).

Marginal and conditional R^2 values indicated that species traits explained between 48% and 63% of between-species variance in F, L and S, while nested phylogenetic random effects explained a further 18-27% of variance (Table 2). The best model for survival (S) included positive effects of body mass and association with marine habitats, negative effects of clutch size and migratory status, and significant variation among dietary guilds (Table 1a). Body mass, clutch size, marine association and

diet had similar effects on *F* and *L* (Table 1b & c), whereas the best model for *F* also included a negative effect of freshwater associations (Table 1b), and for *L* a positive effect of range latitude (Table 1c).

Generation lengths and Red List implications

The median generation length (from Equation 4) was found to be 2.99 years, with a range from 1.42 (Double-barred Finch *Taeniopygia bichenovii*) to 27.87 years (Southern Royal Albatross *Diomedea epomophora*) (Table 4). For 6,814 species (61%), generation length is <3.33 years (Appendix S4), so population trends should be assessed over 10 years under Red List Criterion A. All other species require a longer period over which to assess trends. We estimate that in the absence of calculated generation lengths, assessing trends over the period of 10 years (which was used historically in the absence of calculated generation times) would underestimate the number of species qualifying as threatened or Near Threatened on the Red List based on population decline alone (Appendix S5). Using median estimates of decline over 10 years, 156 fewer species would qualify as threatened or Near Threatened under Criterion A than when declines are measured over the longer of 10 years or three generations, equivalent to 6.2% of threatened and Near Threatened bird species listed on the 2018 Red List (Fig. 2). Overall, however, when all Red List Criteria are considered, 2,014 species (18.5%) qualify as threatened or Near Threatened when declines are assessed over 10 years, versus 2,116 (19.4%) when 10 years or three generations are used (i.e. 102 species fewer).

Discussion

Estimating F, L and S

Life history data are lacking for most species. We found it necessary to use data from well-studied species for supporting assessments of less well-known taxa (IUCN 2019). Even then, we could not use age-specific survival and fecundity rates (see below). It is important that a reliable approach is

used to fill missing values for F, L and S. Cooke et al. (2018) found that body mass was twice as important as phylogeny when predicting generation length in antelopes, and therefore recommended that extrapolations should not be based solely on taxonomy for these taxa. For birds, we found that hierarchical extrapolation was a poorer predictor of published values of F, L and S than our preferred model (Fig. 1), supporting the assertion that allometric and ecological data should be included when predicting life histories and generation lengths (Cooke et al. 2018). We provide a global dataset of F, L and S for all birds (Appendix S2).

Calculating generation length

For most bird species it is believed that the probability of an individual dying is independent of their age (a Type II survivorship curve; Pinder et al., 1978), at least for adults, so we made the assumptions in G_{FLS} of constant fecundity and survival between the ages of first reproduction and maximum longevity. Although invalid for many species because survival and fecundity change gradually with age (Jones et al. 2014), the pattern of change with age is unknown for almost all bird species (Sæther & Bakke 2000).

Assuming that annual survival rate is constant from birth to age L, the proportion of individuals reaching age L is S^L. If S^L is a very small number, this may indicate that S is underestimated. For example, if $S^L = 10^{-7}$, then observing an individual as old as L would require observing millions of individuals. Since such a large sample size is unlikely, S may have been underestimated, resulting in an underestimated generation length. This may happen in various ways: if survival rate declines with age, and S is estimated based mostly on data from older adults. It may also happen if S is apparent survival, which means it does not include a correction for emigration (Ryu et al. 2016). Finally, S may underestimate adult survival rate if it is based on a mixture of juvenile and adult birds, as juveniles have a lower survival rate (Benson et al. 2018).

To avoid underestimation of generation length, we estimated G as the larger of two values, G_{FLS} and G_{FL}. This affected few species: $G_{FL}-G_{FLS} >1$ for only 545 species (4.9% of all species). For these 545 species, S^L ranged from 10^{-25} to 0.039 (average=0.002). In other words, using G_{FL} made a non-negligible difference to the result only for species for which S^L was low. As discussed, we suspect that S is underestimated for many of these species (resulting in an underestimated G_{FLS}). The impact of this underestimation is minimized by use of the larger of G_{FLS} and G_{FL}, but not negated entirely when L has been underestimated. Overall, we assume that divergences from the assumption that fecundity is constant between F and L cancel out – i.e. any tendency to underestimate L because of age-related biases in mark-recapture studies (Mills 2016) or lower fecundity in younger birds, particularly in long-lived species (Curio 1983), is cancelled out by senescence (Nussey et al. 2008). Also, although Cooke et al. (2018) argued that L should only be estimated from wild animals, we have used all longevity data available: current research suggests that longevity is species specific and is mediated partly by genetics and partly by environmental stressors (Vágási et al. 2019). Captivity can be considered the benign end of a continuum, rather than a condition that cannot be replicated in nature, and we assume that including estimates of longevity from captive individuals biases the results upwards no more than a failure to discover the oldest breeding individuals in wild populations biases the results downwards.

The method developed here has attempted to control for variation between particularly well- or poorly-studied species. It is not easy to assess the effectiveness of our approach, but some generation lengths intuitively seem lower or higher than expected. For example, we found no published estimates of F, L, or S for any of the four *Pseudobulweria* petrel species. Their mean generation length of 6.1 years is the lowest of any genus in the *Procellariidae*, half that of the family mean of 12.3 years, and well below the mean generation length of their phylogenetic sister-group *Puffinus* (Bretagnolle & Pasquet 1998) of 12.7 years (Appendix S4). Of the 17 species in the genus *Apus*, the generation length of Common Swift *A. apus* (8.0 years) is 82% higher than the genus mean (4.4 years), while all generation lengths of the other 16 species fall within 17% of the mean. Similarly, of the 99 species in the genus *Zosterops*, the generation length of Silvereye *Z. lateralis* (3.5 years) is 74% higher than the

genus mean (2.0 years), while all other species' generation lengths are within 22% of the mean. Interestingly, in Google searches for "scientific name" for each species in *Apus* and *Zosterops,* Common Swift and Silvereye rank first in their genera for number of hits—a proxy for interest (Nghiem et al. 2016). For both species, generation length came from G_{FL} and they had longevity estimates far in excess of any congeners (Appendix S4). These examples suggest that estimates of generation length (and in particular maximum longevity) of well-studied species may exceed those of the majority of closely related species, and that generation length may hence have been underestimated for many species. Therefore, as new life history data become available, our generation length estimates should be updated to improve their accuracy. Among these, the highest priorities to investigate are those species that have generation length derived from modelled values that are significantly shorter than species in the same subfamily for which data was available: 394 species have values falling below others within their subfamily by more than 50% (Appendix S4) and require attention before their use in Red List assessments.

Generation lengths and Red List implications

After population size, trends are the best predictor of time to extinction, when scaled by generation length (O'Grady et al. 2008). For birds, scaling population trends by generation length has only a modest impact on their estimated overall risk of extinction. The fixed-length period of 10 years appears to be a remarkably good proxy for biological scaling of rates of decline in birds, being very close to the average of three generation lengths. However, for some families, genera and species, it has a substantial impact. Of the 52 species whose rates of decline exceed the threshold for listing as Critically Endangered under Criterion A when measuring trends over the longer of three generations or 10 years, only 30 (58%) would qualify as CR under Criterion A if trends were measured over 10

years. For example, an additional 8 of 22 albatrosses *Diomedeidae* qualify as threatened or Near Threatened under Criterion A when generation lengths are used to scale trends. The number of cockatoos *Cacatuidae* qualifying as threatened or Near Threatened only increases from seven to eight when trends are scaled by generation length, but the number of species qualifying as Critically Endangered or Endangered increases from two to six. Incorporating generation lengths in conservation assessments in this way has obvious consequences for policy and management. Multilateral conventions such as the Convention on Migratory Species, the Agreement on the Conservation of Albatrosses and Petrels (ACAP) and the Convention on International Trade in Endangered Species (CITES) were created to address the elevated extinction risk faced by particular suites of species—extinction risks that are best evaluated by scaling population trends by generation lengths.

The vast majority of bird species' populations and distributions considerably exceed the thresholds for qualifying as threatened under Criteria B, C or D of the Red List. However, many of these currently Least Concern species are declining (3,004/7,719 Least Concern species with known direction of trend = 38.9%; BirdLife International 2018b) Given the widespread and pervasive threats facing birds worldwide, it is not unreasonable to expect that the majority of genuine Red List category changes in future will be species in this pool qualifying for uplisting to higher categories of threat as rates of population decline increase and exceed Red List category thresholds. To date this has not been the case (de L. Brooke et al. 2008; Monroe et al. 2019), but early assessments of birds lacked estimates of generation length for scaling trends. The availability of a global dataset from this study and the incorporation of these new generation lengths into BirdLife's Red List assessments will improve their consistency and accuracy. Approaches like monitoring rates of habitat change and inferring rates of population change for associated species (e.g. Bird et al. 2012; Tracewski et al. 2016), calculating changes in population abundance from citizen-science monitoring (e.g. Wotton et al. 2017; Gregory et al. 2019), and modelling future rates of change from mechanistic studies of the impacts of climate change on species (e.g. Foden et al. 2019; Wauchope et al. 2017) will all allow for improved assessments of extinction risk when generation lengths are used to scale population trends.

In conclusion, this is the first study to calculate generation lengths for all the world's birds: a dataset that provides a comprehensive resource for avian life history studies. Our method for imputing missing life history data and minimising the impacts of data limitations on generation length estimates is not bird-specific and could usefully be applied to other taxa.

Acknowledgments

Supporting Information

Published values of F, L and S and the original source (Appendix S1), published (observed), modelled and extrapolated values of F, L and S (Appendix S2), a database of avian life-history traits recorded for individual species (Appendix S3), calculated G_{FLS}, G_{FL}, G_{FS} and G for all birds (noting those considered priorities for research prior to the adoption of the G for Red List assessments) (Appendix S4), and revised Red List trend estimates with predicted qualifying Red List categories for all birds (Appendix S5) 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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Table 1 Results of model selection predicting annual adult survival (a), age at first reproduction (b) and maximum longevity (c) for the global avifauna[a,b].

a)	Annual adult survival (*S*)									
Rank	Intercept	Diet	Forest	Freshwater	Marine	Migrant	Latitude	Clutch	Mass	ΔAIC	AICw
1	0.61	+			0.26	-0.12		-0.31	0.44	0	0.24
2	0.61	+		-0.05	0.27	-0.12		-0.31	0.44	1.01	0.14
3	0.63	+	-0.04		0.24	-0.13		-0.31	0.44	1.48	0.11
4	0.6	+			0.26	-0.11	-0.01	-0.31	0.44	1.57	0.11
5	0.64	+	-0.05	-0.06	0.26	-0.12		-0.31	0.44	2.25	0.08
6	0.61	+		-0.05	0.28	-0.1	-0.01	-0.3	0.44	2.58	0.07
7	0.63	+	-0.04		0.25	-0.11	-0.01	-0.31	0.44	3.04	0.05
8	0.64	+	-0.05	-0.06	0.26	-0.11	-0.01	-0.3	0.44	3.79	0.04
9	0.58	+			0.25		-0.03	-0.31	0.44	3.91	0.03
10	0.59	+		-0.06	0.27		-0.03	-0.3	0.44	4.54	0.02
b)	Age at first reproduction (*F*)									
Rank	Intercept	Diet	Forest	Freshwater	Marine	Migrant	Latitude	Clutch	Mass	ΔAIC	AICw
1	0.16	+		-0.02	0.04			-0.01	0.13	0	0.21
2	0.16	+		-0.02	0.04		0	-0.01	0.13	0.28	0.18
3	0.16	+		-0.02	0.04	0.01	-0.01	-0.01	0.13	1.92	0.08
4	0.15	+	0	-0.02	0.04			-0.01	0.13	1.93	0.08
5	0.15	+		-0.02	0.04	0		-0.01	0.13	2.04	0.07
6	0.16	+	0	-0.02	0.04		0	-0.01	0.13	2.17	0.07
7	0.15	+			0.04		0	-0.01	0.13	2.31	0.07
8	0.15	+			0.04			-0.01	0.13	2.53	0.06
9	0.15	+	0	-0.02	0.04	0.01	-0.01	-0.01	0.13	3.8	0.03
10	0.15	+	0.01		0.04		0	-0.01	0.13	3.95	0.03
c)	Maximum longevity (*L*)									
Rank	Intercept	Diet	Forest	Freshwater	Marine	Migrant	Latitude	Clutch	Mass	ΔAIC	AICw
1	1.05	+			0.04		0.02	-0.04	0.13	0	0.29
2	1.06	+	-0.01		0.04		0.02	-0.04	0.13	0.92	0.18
3	1.05	+		-0.01	0.04		0.02	-0.04	0.13	1.8	0.12

4	1.05	+			0.04	0.01	0.02	-0.04	0.13	1.8	0.12
5	1.06	+	-0.01	-0.01	0.04		0.02	-0.04	0.13	2.54	0.08
6	1.06	+	-0.01		0.04	0	0.02	-0.04	0.13	2.79	0.07
7	1.05	+		-0.01	0.04	0.01	0.02	-0.04	0.13	3.55	0.05
8	1.06	+	-0.01	-0.01	0.04	0.01	0.02	-0.04	0.13	4.36	0.03
9	1.06	+	-0.02				0.03	-0.04	0.14	5.6	0.02
10	1.05	+					0.03	-0.04	0.14	6.37	0.01

[a] The 10 top-ranked models (using AICc) for each response variable are shown, indicating the parameters included in the model and their coefficients (except for multi-level categorical predictors, where those marked "+" were included).

[b] All models included Order, Family and Genus as nested random effects.

Table 2 Explanatory power of models determined using methods of Nakagawa & Schielzeth (2013) [a,b].

Response variable	Marginal R^2	Conditional R^2
Annual adult survival (*S*)	0.581	0.767
Age at first reproduction (*F*)	0.629	0.890
Maximum longevity (*L*)	0.479	0.658

[a] Marginal R^2 values show the proportion of variance explained by fixed effects (in this case, species traits), while conditional R^2 shows the variance explained by fixed and random effects combined (i.e. including phylogeny).

[b] Values show the best models for each response from the candidate sets that included clutch size as a predictor.

Table 3: Mean *z* values based on published values of *F*.

F	Number of species	Mean z	StdDev of z
0.5-1.5	301	0.142	0.0536
1.5-2.5	79	0.194	0.0748
2.5-4.5	102	0.236	0.0697
>4.5	68	0.317	0.0602

Table 4: Families and species that have the longest and shortest generation lengths.

10 families with longest generation lengths			10 families with shortest generation lengths		
Diomedeidae	Albatrosses	21.73	Pardalotidae	Pardalotes	2.12
Struthionidae	Ostriches	14.53	Trochilidae	Hummingbirds	2.09
Cacatuidae	Cockatoos	13.94	Viduidae	Whydahs and indigobirds	2.05
Fregatidae	Frigatebirds	13.39	Estrildidae	Waxbills	2.05
Cathartidae	New World vultures	13.21	Remizidae	Penduline-tits	1.99
Pelecanidae	Pelicans	12.56	Phylloscopidae	Leaf-warblers	1.98
Gruidae	Cranes	12.51	Polioptilidae	Gnatcatchers	1.94
Stercorariidae	Skuas	12.45	Certhiidae	Treecreepers	1.89
Phoenicopteridae	Flamingos	12.35	Regulidae	Kinglets and firecrests	1.83
Procellariidae	Petrels, shearwaters	12.26	Elachuridae	Elachura	1.82
10 species with longest generation lengths			10 species with shortest generation lengths		
Diomedea epomophora	Southern Royal Albatross	27.87	*Atthis heloisa*	Bumblebee Hummingbird	1.59
Vultur gryphus	Andean Condor	27.25	*Lonchura caniceps*	Grey-headed Mannikin	1.57
Cacatua galerita	Sulphur-crested Cockatoo	27.21	*Taeniopygia guttata*	Timor Zebra Finch	1.57
Phoebastria immutabilis	Laysan Albatross	26.70	*Margaroperdix madagarensis*	Madagascar Partridge	1.53
Diomedea sanfordi	Northern Royal Albatross	25.97	*Colinus cristatus*	Crested Bobwhite	1.53
Diomedea antipodensis	Antipodean Albatross	25.86	*Estrilda perreini*	Black-tailed Waxbill	1.50
Strigops habroptila	Kakapo	25.82	*Perdix dauurica*	Daurian Partridge	1.49
Fulmarus glacialis	Northern Fulmar	25.34	*Sublegatus obscurior*	Amazonian Scrub-flycatcher	1.46
Cacatua moluccensis	Salmon-crested Cockatoo	24.19	*Rhipidura albicollis*	White-throated Fantail	1.44
Thalassarche melanophris	Black-browed Albatross	23.61	*Taeniopygia bichenovii*	Double-barred Finch	1.42

Figure 1: Published versus predicted values of *F*, *L*, and *S* based upon taxon means from hierarchical extrapolation (above), and modelled values (below). Solid lines represent the plotted relationship between published and predicted values while dotted lines trace a perfect relationship.
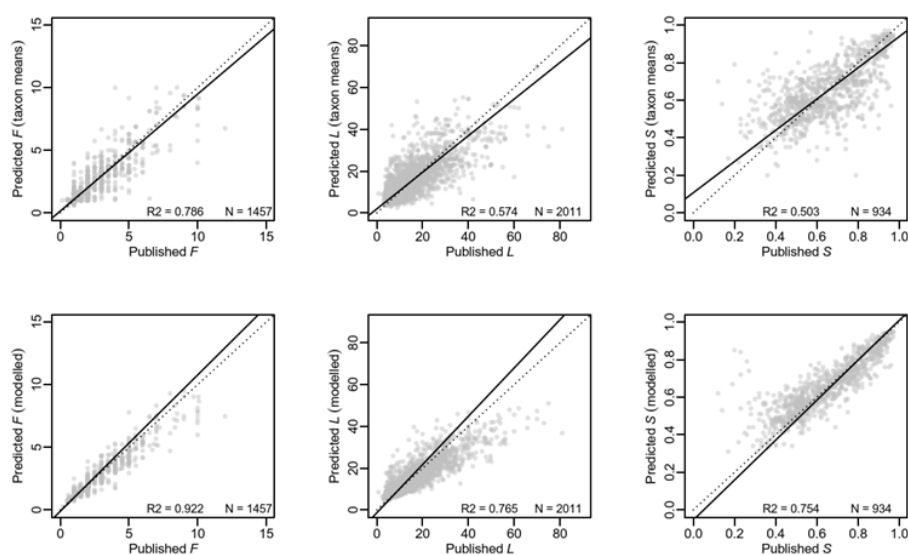
Figure 2: Red List implications of calculating trends over three generations using the newly estimated generation lengths: a) for species qualifying only owing to population declines under Criterion A; b) for species qualifying under any Red List Criteria. Bars show the number of species qualifying for each Red List category (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened) when assessing trends over 10 years (black), three generations (grey).