

Contributed Paper

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

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Abstract: Birds have been comprehensively assessed on the International Union for Conservation of Nature (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 criteria of the IUCN Red List. 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 with generalized linear mixed models. Generation lengths were derived for all species, based on our modeled values of age at first breeding, maximum longevity, and annual adult survival. The resulting generation lengths varied from 1.42 to 27.87 years (median 2.99). Most species (61%) had generation lengths <3.33 years, meaning that the period of 3 generations—over which population declines are assessed under criterion A—was <10 years, which is the value used for IUCN Red List assessments of species with short generation times. For these species, our trait-informed estimates of generation length suggested that 10 years is a robust precautionary value for threat assessment. In other cases, however, for whole families, genera, or individual species, generation length had a substantial impact on their estimated extinction risk, resulting in higher extinction risk in long-lived species than in short-lived species. Although our approach effectively addressed data gaps, generation lengths for some species may have been underestimated due 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.

Keywords: extinction risk, longevity, IUCN red list, species assessment, survival

Duraciones Generacionales de las Aves del Mundo y sus Implicaciones para el Riesgo de Extinción

Resumen: Las aves han sido valoradas integralmente en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) más veces que cualquier otro grupo taxonómico. Sin embargo, a la fecha, las duraciones generacionales no han sido estimadas sistemáticamente para escalar las tendencias poblacionales cuando se realizan las valoraciones, como lo requieren los criterios de la Lista Roja de la UICN. Compilamos información a partir de las principales bases de datos de historias de vida y datos de características publicadas para todas las aves e imputamos los datos faltantes de historias de vida como una función de las características de especies con modelos lineales mixtos generalizados. La duración por generación estuvo derivada para todas las

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especies con base en nuestros valores modelados de edad durante la primera reproducción, la longevidad máxima y la supervivencia anual de adultos. La duración por generación resultante varió de 1.42 a 27.87 años (mediana: 2.99). La mayoría de las especies (61%) tuvo una duración generacional <3.33 años, lo que significa que el periodo de tres generaciones - durante el cual se valoran las declinaciones poblacionales bajo el Criterio A - es <10 años, el cual es el valor usado por la Lista Roja de la UICN para la valoración de especies con tiempos generacionales cortos. Para estas especies, nuestras estimaciones de duración por generación informados por características sugieren que diez años es un valor preventivo sólido para la valoración de amenazas. Para otros casos, sin embargo, como familias o géneros enteros o especies individuales, la duración generacional tuvo un impacto sustancial sobre su riesgo de extinción estimado, resultando así en un riesgo de extinción más elevado para las especies con mayor longevidad que aquellas especies con una menor longevidad. Aunque nuestra estrategia lidió efectivamente con los vacíos en los datos, la duración generacional para algunas especies podría estar subestimada debido a la escasez de datos de historia de vida. En general, nuestros resultados fortalecerán las futuras valoraciones de extinción de riesgo y aumentarán las bases de datos importantes de la historia de vida de las aves y los datos de características.

Palabras Clave: evaluación de especies, lista roja, longevidad, riesgo de extinción, valoración de especie

摘要: 在《世界自然保护联盟 (IUCN) 濒危物种红色名录》中, 鸟类被全面评估的次数比其它任何类群都要多。然而, 目前的评估尚未按照《IUCN红色名单》标准的要求, 系统地估计世代时间来计算种群趋势。我们从已发表的所有鸟类生活史及特征数据的几大数据库中整理了信息, 并用广义线性混合模型构建物种特征的函数对缺失的生活史数据进行了估计。我们进而基于对初次繁殖年龄、最长寿命和成体年均存活率的模拟值, 获得了所有物种的世代时间。得到的鸟类世代时间从 1.42 年到 27.87 年不等 (中位数为 2.99 年)。大多数物种 (61%) 的世代时间小于 3.33 年, 意味着三个时代的时长小于 10 年, 而这是《IUCN 红色名录》评估标准 A 中对种群下降的评估周期, 用于评估世代时间短的物种。对于这些物种, 基于特征估计的世代时间表明, 10 年是评估威胁的一个稳健预警值。而在其他情况下, 世代时间对于估计整个科、属或个别物种的灭绝风险有重大影响, 结果导致寿命长的物种灭绝风险高于寿命短的物种。虽然我们的方法有效地解决了数据缺失的问题, 但由于一些物种生活史数据缺乏, 其世代时间可能会被低估。总的来说, 我们的研究结果将强化未来的灭绝风险评估, 并扩增鸟类生活史和特征数据的关键数据库。【翻译: 胡怡思; 审校: 聂永刚】

关键词: 红色名录, 灭绝风险, 寿命, 存活, 物种评估

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 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 used 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, the 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; recovery rates of marked individuals are declining (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 International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter 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 6 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.

Quantitative criteria are used to assign species to categories of relative extinction risk on the red list 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 for the red list. This is particularly important under red list criterion A, which covers declines over 10 years or 3 generations, whichever is longer, and criterion C, which covers population size, structure, and trends scaled by generation length (IUCN 2012). Because generation lengths have hitherto not been estimated systematically and consistently for all bird species on the red list, we used available data to estimate F , L , and S for all birds, and from these parameters we derived estimates of generation lengths. We then assessed the implications of our derived generation lengths for the red list, in terms of the number of species qualifying within each category, when trends are scaled over 3 generations.

Methods

Data Collation and Modeling

We compiled a data set of published values for F , L , and S from a variety of sources (Supporting Information). We compared 2 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 congeners, 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 was used; and when there were no published estimates for the entire family, the mean of other values for the order was used (Supporting Information). 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 P_i . We calculated R^2 between the published and predicted values.

Second, we used a modeling approach. Each of F , L , and S is correlated with a range of species traits, including body size, and constraints associated with the environments species inhabit (Partridge & Harvey 1988; Sæther & Bakke 2000). We used selected avian species traits (Supporting Information) to model variation in F , L , and S as a function of species traits and 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 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 3 response parameters. We also included breeding-range

centroid latitudes (as absolute values, derived from BirdLife's global species distribution maps) (BirdLife International 2018b) 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 for which estimates were available ($n = 2156$ of 2401 species with data on F , L , or S). We centered 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 $2\Delta\text{AIC}_c$ 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, whereas F and L were log transformed and modeled as Gaussian responses (Quinn & Keough 2002). All models were fitted in R statistics version 3.3.1 with 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 and Schielzeth (2013). Having confirmed that the models performed adequately in explaining observed variation in F , L , and S across species in the data set (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 9484 species worldwide (Supporting Information), with the exception of clutch size, which was missing for 3386 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 1642 species lacking data on 2 or more necessary traits for model prediction, we assigned values of F , L , and S by using the means of other species in that genus, family, or order, depending on the availability (i.e., hierarchical extrapolation).

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

Calculating Generation Lengths

We used the model-predicted values of F , L , and S (Supporting Information) to estimate generation length in 2 ways: based on F , L , and S (G_{FLS}) (Eq. 1) and based on F and L (G_{FL}) (Eq. 2):

$$G_{FLS} = \frac{\sum_{x=F}^L x l_x}{\sum_{x=F}^L l_x}, \quad (1)$$

Table 1. Results of model selection predicting annual adult survival, age at first reproduction, and maximum longevity for global avifauna^a.

Life-history trait	Rank	Intercept	Forest	Freshwater	Marine	Migrant	Latitude	Clutch	Mass	ΔAIC	AICw
Annual adult survival	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
Age at first reproduction	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
Maximum longevity	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

^aThe 10 top-ranked models based on Akaike information criterion (AICc) for each response variable are shown, including parameters included in the model and their coefficients. The multilevel categorical predictor of diet was included for all top-10 models. All models included order, family, and genus as nested random effects.

where x is age in years; summations are from age (x) of first reproduction (F) to maximum longevity (L); and I_x is survival up to age x (i.e., $I_x = S_0 \cdot S_1 \cdots S_{x-1}$, where S is annual survival rate and $I_0 = 1$ by definition [IUCN 2019]). We assumed $I_x = S^x$ (see below):

$$G_{FL} = F + z(L - F), \quad (2)$$

where z is a number between 0 and 1 (IUCN 2019). To calculate z , we used Eq. 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 with

$$z = (G_{FLS} - F_{\max}) / (L_{\max} - F_{\max}), \quad (3)$$

where F_{\max} and L_{\max} are, for each species, the maximum of either the observed value or the modeled value. We calculated the average value of z for 4 groups (Table 3), based on published F , and used these average values in Eq. 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 is based on the assumption that

fecundity is 0 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, Eq. 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 $I_x = S^x$. Because Eq. 1 can result in an underestimate of generation length under certain conditions (see Discussion) and because this may affect the calculation of z (because Eq. 3 uses G_{FLS}), we defined generation length of each species as the larger of the 2 estimates (Supporting Information):

$$G = \max(G_{FLS}, G_{FL}), \quad (4)$$

For each species, we also calculated the difference between the 2 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 assumed the data sources we used likely defined age such that an individual starting to breed (nesting and mating) at < 12 months of age in the breeding season after the one in which it fledged is called 1 year old,

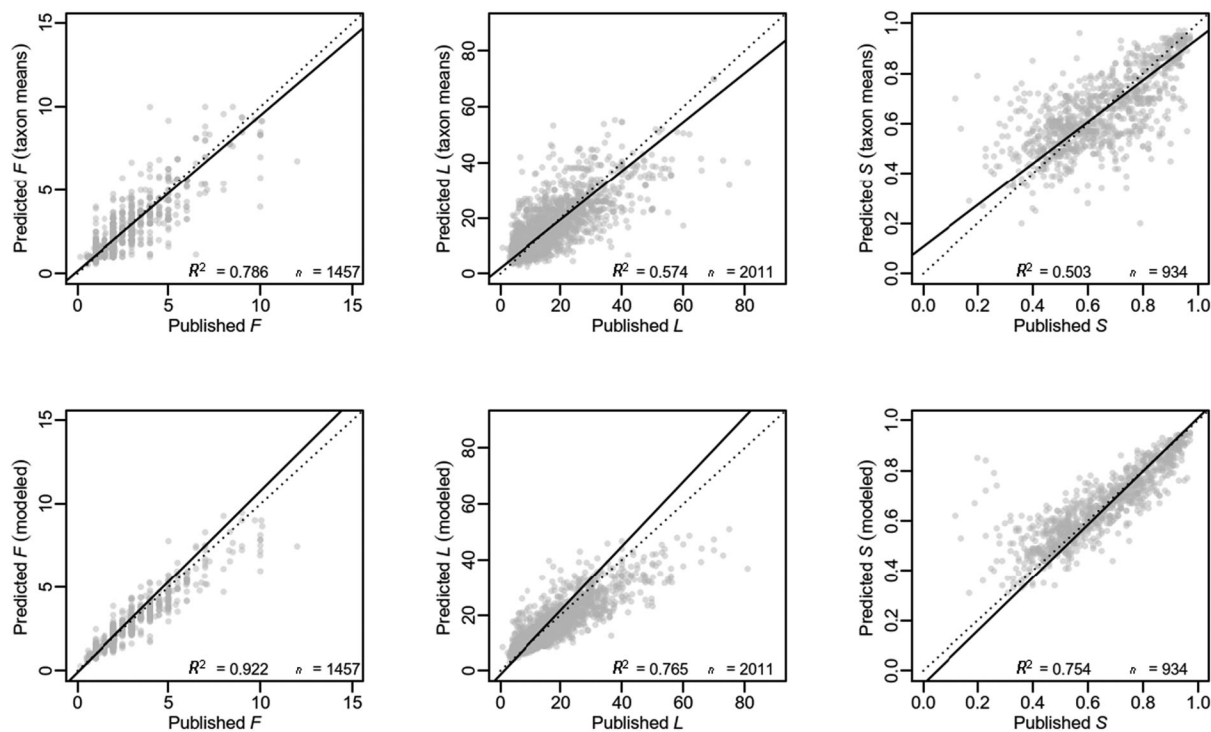


Figure 1. Published versus predicted values of age at first reproduction (F), maximum longevity (L), and annual adult survival (S) based on taxon means from hierarchical extrapolation (above) and modeled values (below) (solid lines, plotted relationship between published and predicted values; dotted lines, perfect relationship).

Table 2. Explanatory power of models of annual adult survival, age at first reproduction, and maximum longevity at predicting published values of these 3 parameters, determined using methods of Nakagawa and Schielzeth (2013)*.

Response variable	Marginal R^2	Conditional R^2
Annual adult survival	0.581	0.767
Age at first reproduction	0.629	0.890
Maximum longevity	0.479	0.658

* Marginal R^2 values show the proportion of variance explained by fixed effects (in this case, species traits), whereas conditional R^2 shows the variance explained by fixed and random effects combined (including phylogeny). Values are for the best models for each response from the candidate sets that included clutch size as a predictor.

Table 3. Mean z values calculated for species with published estimates of annual adult survival (S) > 0.3 or S raised to the power of maximum longevity (S^L) of $> 10^{-5}$ (see methods) grouped according to published values of age at first reproduction (F).

F	Number of species	Mean z	SD 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

which is different from the definition used in the red-list guidelines (IUCN 2019) and the workbook accompany-

ing 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 we used. This formulation (also known as the adult mortality proxy) is based on the assumption 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 Implications for Extinction Risk Assessment

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 3 generations (Supporting Information). These trend estimates represent a percent population decline or increase over 10 years or 3 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 3 generations) because 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 times 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 $T_2 = \max(10 \text{ years}, 3 \text{ generations})$, 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% were inferred because none of these species are listed as threatened or near threatened under criterion A (Supporting Information), whereas species with a rate of decline of $\geq 25\%$ over 10 years or 3 generations are candidates for near threatened or threatened status (IUCN 2019). Median estimates were calculated as the midpoint 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 2 values for each minimum, median, and maximum trend estimate for each species. Each species was given an overall minimum, median, and maximum based on 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; and 30–49% decline, vulnerable (IUCN 2012). We derived a threshold of 25–29% decline for 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

Estimates of 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 ex-

tant bird species, respectively (Supporting Information). 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 (Supporting Information). However, extrapolated values were poorer at predicting published estimates than were modeled values (Fig. 1).

Marginal and conditional R^2 values indicated that species traits explained 48–63% of between-species variance in F , L , and S , whereas nested phylogenetic random effects explained a further 18–27% of variance (Table 2). The best model for 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 1). Body mass, clutch size, marine association, and diet had similar effects on F and L , whereas the best model for F also included a negative effect of freshwater associations and for L a positive effect of range latitude (Table 1).

Generation Lengths and Implications for Extinction Risk Assessment

The median generation length (from Eq. 4) was 2.99 years. The range was from 1.42 (Double-barred Finch [*Taeniopygia bichenovii*]) to 27.87 years (Southern Royal Albatross [*Diomedea epomophora*]) (Table 4). For 6814 species (61%), generation length is <3.33 years (Supporting Information), 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 estimated that in the absence of calculated generation lengths, assessing trends over 10 years (which was used historically in the absence of calculated generation times) underestimated the number of species qualifying as threatened or near threatened on the red list based on population decline alone (Supporting Information). Using median estimates of decline over 10 years, 156 fewer species qualified as threatened or near threatened under criterion A than when declines were measured over the longer of 10 years or 3 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 were considered, 2014 species (18.5%) qualified as threatened or near threatened when declines were assessed over 10 years, versus 2116 (19.4%) when 10 years or 3 generations was used (i.e., 102 species fewer).

Discussion

Estimates of F , L , and S

Life-history data are lacking for most species. We found that it is necessary to use data from well-studied species

Table 4. Ten avian families and ten avian species with the longest and shortest generation lengths.

Longest generation length		Years	Shortest generation length		Years
Family					
Diomedidae	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	Poliophtilidae	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
Species					
<i>Diomedea epomophora</i>	Southern Royal Albatross	27.87	<i>Atthis beloisia</i>	Bumblebee Hummingbird	1.59
<i>Vultur gryphus</i>	Andean Condor	27.25	<i>Lonchura caniceps</i>	Grey-headed Mannikin	1.57
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	27.21	<i>Taeniopygia guttata</i>	Timor Zebra Finch	1.57
<i>Phoebastria immutabilis</i>	Laysan Albatross	26.70	<i>Margaroperdix madagarensis</i>	Madagascar Partridge	1.53
<i>Diomedea sanfordi</i>	Northern Royal Albatross	25.97	<i>Colinus cristatus</i>	Crested Bobwhite	1.53
<i>Diomedea antipodensis</i>	Antipodean Albatross	25.86	<i>Estrilda perreini</i>	Black-tailed Waxbill	1.50
<i>Strigops habroptila</i>	Kakapo	25.82	<i>Perdix dauurica</i>	Daurian Partridge	1.49
<i>Fulmarus glacialis</i>	Northern Fulmar	25.34	<i>Sublegatus obscurior</i>	Amazonian Scrub-flycatcher	1.46
<i>Cacatua moluccensis</i>	Salmon-crested Cockatoo	24.19	<i>Rhipidura albicollis</i>	White-throated Fantail	1.44
<i>Thalassarche melanophrys</i>	Black-browed Albatross	23.61	<i>Taeniopygia bichenovii</i>	Double-barred Finch	1.42

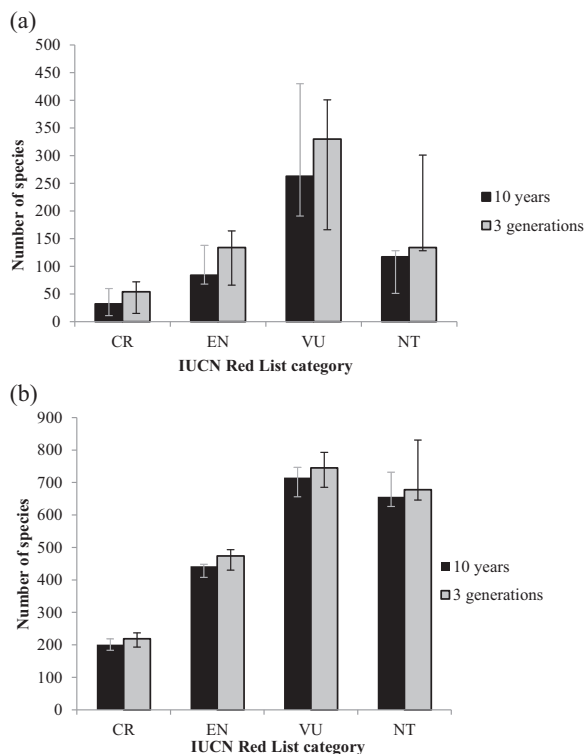


Figure 2. Number of species qualifying in each International Union for the Conservation of Nature (IUCN) Red List category when population trends are scaled over 10 years or 3 generations for (a) partial assessments based only on IUCN Red List criterion A thresholds and (b) full assessments based on all IUCN Red List criteria (CR, critically endangered; EN, endangered; VU, vulnerable; and NT, near threatened).

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 be used to fill missing values for F , L , and S . Cooke et al. (2018) found that body mass is twice as important as phylogeny when predicting generation length in antelopes and, therefore, recommends 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 data set of F , L , and S for all birds in Supporting Information.

Generation Length

For most bird species, it is believed that the probability of an individual dying is independent of its age (a type II survivorship curve [Pinder et al. 1978]), at least for adults, so we assumed for G_{FLS} 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. Because such a large sample size

is unlikely, S may have been underestimated, resulting in an underestimated generation length. This may happen in various ways, for example, 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 because juveniles have a lower survival rate (Benson et al. 2018).

To avoid underestimation of generation length, we estimated G as the larger of 2 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. 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 the use of the larger of G_{FLS} and G_{FL} , but not negated entirely when L has been underestimated. Overall, we assumed that divergences from the assumption that fecundity is constant between F and L cancel out; that is, 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). Although Cooke et al. (2018) argue that L should only be estimated from wild animals, we 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 upward no more than a failure to discover the oldest breeding individuals in wild populations biases the results downward.

We 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 4 *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 (Supporting Information). 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), whereas 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), whereas all other species' generation lengths are within 22% of the mean.

Interestingly, in Google searches for the scientific name of 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 (Supporting Information). 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 modeled values that are significantly shorter than species in the same subfamily for which data were available: 394 species have values below others within their subfamily by more than 50% (Supporting Information) and require attention before they can be assessed for the red list.

Generation Lengths and Implications for Extinction Risk Assessment

After population size, population 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 period of 10 years appears to be a remarkably good proxy for biological scaling of rates of decline in birds; it is very close to the average of 3 generation lengths. However, for some families, genera, and species, it has a substantial impact. Of the 52 species whose rates of decline exceeded the threshold for listing as critically endangered under criterion A when measuring trends over the longer of 3 generations or 10 years, only 30 (58%) qualified as CR under criterion A when trends were measured over 10 years. For example, an additional 8 of 22 albatrosses *Diomedidae* qualified as threatened or near threatened under criterion A when generation lengths were used to scale trends. The number of cockatoos *Cacatuidae* qualifying as threatened or near threatened only increased from 7 to 8 when trends were scaled by generation length, but the number of species qualifying as critically endangered or endangered increased from 2 to 6. 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 (3004 of 7719 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 (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 data set from this study and the incorporation of these new generation lengths into BirdLife's red-list assessments will improve their consistency and accuracy. Approaches, such as 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 modeling future rates of change from mechanistic studies of the impacts of climate change on species (e.g., Wauchope et al. 2017; Foden et al. 2019), will all allow for improved assessments of extinction risk when generation lengths are used to scale population trends.

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

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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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