Title: Performance of generation time approximations for extinction risk assessments

Authors:
Johanna Staerk\textsuperscript{1,2,3,4}, Dalia A. Conde\textsuperscript{1,2,3}, Victor Ronget\textsuperscript{5}, Jean-François Lemaitre\textsuperscript{5}, Jean-Michel Gaillard\textsuperscript{5}, Fernando Colchero\textsuperscript{1,6}

Affiliations: \textsuperscript{1}Species360 Conservation Science Alliance, 7900 International Drive, Suite 1040 Bloomington, MN, 55425 USA. \textsuperscript{2}Interdisciplinary Centre on Population Dynamics, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark. \textsuperscript{3}Department of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark. \textsuperscript{4}Max Planck Institute for Demographic Research, Konrad-Zuse-Strasse 1, D-18057, Rostock, Germany. \textsuperscript{5}University of Lyon, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France. \textsuperscript{6}Department of Mathematics and Computer Science, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark.

Correspondence: Johanna Staerk, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark, Johanna.staerk@species360.org

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Abstract:
1. Generation time is a fundamental component of extinction risk assessments for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Calculation of generation time requires age-specific data on survival and fecundity rates and knowledge of population growth rates. These data are generally lacking for threatened species, so approximations including only partial demographic information need to be used. This leads to potential errors in generation time estimates.

2. To quantify the magnitude of potential errors in generation time estimates, we compared seven approximations with exact generation time measures, calculated either from complete life tables available for 58 mammalian species or from simulated data. We tested the influence of these errors on conservation assessments conducting mock assessments for ten species. We also tested the commonly used prediction of generation time based on the allometric relationship with body mass using phylogenetic generalized least squares.

3. Root-mean-square errors were largest in measures assuming constant fecundity with age, some of which are currently used in Red List assessments. We found that the measure of generation time that only ignores population growth rates performed relatively well, but tended to under-estimate generation time for decreasing populations, and over-estimate it for increasing populations.

4. In the mock assessment, we found that we underestimated the threat level in 10% to 90% of the species depending on the generation time approximation we used.

5. The predictive metric of generation time based on body mass is inaccurate. We propose an alternative predictive metric based on body mass, age at first reproduction, and reproductive lifespan.
6. **Synthesis and applications.** Our results demonstrate potential errors that occur when estimating generation time in absence of key demographic information. We offer practical recommendations for extinction risk assessments including more rigorous mathematical formulations of generation time, such as the measure of generation time that includes population growth rates and the appropriate age-specific vital rates. Furthermore, we recommend alerting risk assessors of the uncertainties in proxy measures, such as the underestimation of generation time resulting from the assumption of constant fecundity in future Red List assessments.

**Introduction**

Population demography is extremely variable across species and environments, as demonstrated by the diversity of age-specific trajectories of survival and fecundity across the tree of life (Jones et al., 2014). Identifying these trajectories allows researchers to estimate key measures of population dynamics such as population growth rates and generation time (Caswell, 2001; Gaillard et al., 2005; Tuljapurkar, Gaillard & Coulson, 2009; Bienvenu & Legendre, 2015). Three main definitions of generation time include: (1) the time required for a population at the stable age distribution to grow by the net reproductive rate (Birch, 1948, $T_b$); (2) the mean age of the parents of offspring produced in the current time period once the population has reached the stable age distribution (henceforth the period definition, Leslie, 1966 $T_b$); and (3) the mean age at which members of a cohort of newborns produce offspring (henceforth the cohort definition, Dublin & Lotka, 1925 $T_c$) (Table 1). Generation time has been used in a wide range of applications, including measuring the pace of life across species (Gaillard et al., 2005; Baudisch, 2011), ranking species along the slow-
fast life history continuum (Gaillard et al., 2005), evaluating the response of species to variable environments (Tuljapurkar, Gaillard & Coulson, 2009), calculating evolution rates (Evans et al., 2012), and estimating extinction risk (Mace et al., 2008). Concerning extinction risk, generation time is routinely used as one important factor for species threat assessments by worldwide conservation organizations such as the International Union for Conservation of Nature (IUCN) or to assess bycatch limits in fisheries (Dillingham, 2010). Moreover, generation time influences the mutation rate, making it an indicator for species’ adaptability to climate change (Foden et al., 2013; Pearson et al., 2014). Based on such fundamental role in establishing conservation goals, it is necessary to obtain accurate generation time estimates for endangered species. When the necessary data for such estimation are missing, it is imperative to have a clear understanding of the errors in the available generation time values.

The IUCN Red List of Threatened Species (IUCN, 2017a) is the primary authority for extinction risk assessments. In the Red List assessment, species are categorized as threatened based on criteria related to population decline, geographic range size, fragmentation, and small population size (IUCN, 2017b). In criteria related to population decline, generation time acts as a standardization for time units that allow using the same criteria on species with extremely different lifespans (Mace et al., 2008). In criterion A for example, population size reduction is measured over ten years or three generations, whichever is longer. Therefore, an underestimation of generation time would result in the population reduction being measured over a shorter time period possibly leading to an underestimation of extinction risk, with an opposite effect when overestimating generation time. Such potential inaccuracies could have consequences for many species, because criteria including generation time
have been used to list 41% of mammals, 33% of birds, 14% of amphibians, 19% of reptiles, and 96% of corals categorized as threatened (IUCN, 2017a).

In the *IUCN Guidelines for Using the IUCN Red List Categories and Criteria* (henceforth IUCN guidelines, IUCN, 2017b) generation time measures are commonly based on the cohort definition ($T_c$), which is considered to provide a reasonable approximation to generation time. However, using $T_c$ is only appropriate for data collected from a single cohort, from which individuals are monitored from birth to death, or under the assumption of stationary populations (i.e. a population growth rate equal to one). In many studies of mammals in the wild, however, age-specific vital rates are calculated as averages across years on cross-sectional data (i.e. including multiple cohorts) (e.g. Nussey et al., 2008). Thus, the period approach to calculate generation time ($T_p$) is the most general measure as it accounts for overlapping generations by including the population growth rate.

Both the cohort and the period definitions of generation time require complete age- and sex- specific data on survival and fecundity, but this detailed information is currently available for only ~1.6% of threatened tetrapods and probably even less for other taxonomic groups (Conde et al., unpublished data). Given the scarcity of demographic data, demographic traits such as the average age at first reproduction (Tsantes & Steiper, 2009) or evolutionary allometric relationships between generation time and body mass are frequently used to approximate generation time (Millar & Zammuto, 1983; Gaillard et al., 2005; Cooke et al., 2018).

The IUCN guidelines explicitly mention two alternative generation time approximations: The first is the ‘reproductive lifespan proxy’ that calculates generation time as the sum of age at first reproduction and the product of a variable $z$ and the species reproductive lifespan ($T_z$, Table 1). This variable $z$, bounded between 0
and 1, is estimated as the average from species for which generation time can be accurately estimated, and then used to approximate generation time for species with no demographic information. For example, \( z \) has been fixed at 0.29 (Pacifici et al., 2013) and 0.28 (Keith et al., 2015), for mammals. The \( z \)-value simply states that generation time cannot be smaller than age at first reproduction or larger than the age at last reproduction and, based on the IUCN guidelines, scales accordingly to the relative fecundity of young vs. old individuals in the population. The second measure is the ‘adult-mortality proxy’, which is calculated as the sum of age at first reproduction and the inverse of average annual adult mortality \( (T_q, \text{Table 1}) \). Using these measures facilitates approximating generation time for many species, as the required variables are more commonly available than age-specific vital rates. For example, data on age at first reproduction currently exist for at least 35% of mammals (Conde, et al., unpublished data). However, these measures should be applied under careful consideration as they may lead to considerable errors. For example, Cooke et al. (2018) found that calculating generation time from the ‘reproductive lifespan proxy’ for Bovidae species can lead to erroneous results when the age at last reproduction is estimated based on maximum longevity in captivity rather than in the wild. Such discrepancy comes from the consistently longer life of captive mammals compared to their wild counterparts (Tidière et al., 2016). Moreover, Fung and Waples (2017) reported that the estimation of generation time requires an adjustment, recently incorporated into the IUCN guidelines (2017b), that shifts ages by one year, particularly for species that start reproducing before their first year of age. Ignoring this adjustment may result in biased assessments of currently used generation time proxies. Fung and Waples (2017)’s study provides the first attempt to predict and correct for errors generated by using proxies instead of more accurate generation time
estimates. However, their study stresses the use of approximations bearing many assumptions, such as constant adult mortality and stationary populations, rarely met in wildlife populations.

Here, we review currently used generation time measures and compare the metric of generation time with the least number of assumptions (i.e. the period definition of generation time, $T_b$) to seven metrics including only partial demographic information on real and simulated data. We assess the influence of these errors on IUCN Red List assessments by conducting mock assessments under criterion A for ten mammal populations. We further propose an alternative approach for estimating generation time based on allometric relationships between generation time and some key species-specific life history traits.

**Materials and Methods**

*Life tables from wild populations*

We obtained published life tables of wild populations for 58 terrestrial and marine mammalian species (see Table S1 in Supporting Information). From these we extracted the cumulative survival probability at age $x$ ($l_x$) and the average number of female offspring born to females of age $x$ (i.e. fecundity, $m_x$). We defined $\alpha$ as the age at first reproduction (i.e. first age when $m_x \neq 0$), and $\omega$ as the age when reproduction was last observed. We equated missing values of $m_x$ at older ages to 0 when only a handful of individuals were still alive. From the $l_x$ and $m_x$ data, we built population projection matrices (Caswell, 2001) to calculate the asymptotic population growth rate $\lambda$ (as the dominant eigenvalue) and the corresponding stable age distribution $v$ (as the corresponding right eigenvector). Most life tables started at birth, but in 14 species
survival was lacking prior to age at first reproduction. For these we used estimates of juvenile survival from a different population of the same species (Table S1).

Simulated data

We constructed 15 mortality and 15 fecundity trajectories resulting in 225 life tables, thereby allowing us to explore a wider range of mortality and fecundity combinations than those obtained from field data. We calculated mortality trajectories by varying the mortality or hazard rate function

\[
\mu(x | \theta) = \lim_{\Delta x \to 0} \frac{\Pr(x \leq X < x + \Delta x \mid X \geq x, \theta)}{\Delta x},
\]  

which is the rate at which individuals die as a function of age \( x \), given they survived to the beginning of the interval \([x, x + \Delta x]\), where \( X \) is a random variable for ages at death and \( \theta \) is a vector of mortality parameters. For the different shapes, we varied the parameters of the functions calculated as

\[
\begin{align*}
\mu(x | \theta) = \begin{cases} 
  c & \text{constant mortality} \\
  \exp(a_0 + b_1 x) & \text{increasing mortality} \\
  \exp(a_0 - a_1 x) & \text{decreasing mortality} \\
  \exp(a_0 - a_1 x) + c + \exp(b_0 + b_1 x) & \text{bathtub mortality} \\
  \exp(b_0 + b_1 x) / \left[ 1 + b_2 e^{b_1 x} (e^{b_1 x} - 1) \right] & \text{logistic mortality}
\end{cases}
\end{align*}
\]  

where \( \theta^T = [a_0, a_1, c, b_0, b_1, b_2] \) is the vector of mortality parameters, where \(-\infty < a_0, b_0 < \infty \) and \( a_1, c, b_1, b_2 \geq 0 \). We chose these mortality functions because they produce the most commonly encountered age-specific mortality profiles for vertebrates (Promislow, Montgomerie & Martin, 1992; Ricklefs, 2000; Ricklefs & Scheuerlein, 2001; Bronikowski et al., 2011; Jones et al., 2014; Colchero et al., 2017). The resulting mortality patterns and life expectancy at birth, \( e_0 \), are depicted in Fig. S1.
From the hazard rate, the cumulative survival probability is calculated as

$$S(x | \theta) = \Pr(X > x) = \exp \left[ - \int_{0}^{x} \mu(t | \theta) dt \right].$$  \hfill (3)

Here $S(x)$ provides the expression for $I_x$ in continuous time. From the age-structured mortality rates, we calculated survival probabilities at every age interval as

$$p_x = \Pr(X > x + \Delta x | X > x)$$

$$= \exp \left[ - \int_{x}^{x+\Delta x} \mu(t) dt \right]$$

$$= \frac{S(x + \Delta x)}{S_x},$$ \hfill (4)

where $\Delta x = 1$. We modelled the age-specific fecundity rate using the following flexible exponential function with a quadratic effect as a function of age (Emlen, 1970)

$$m(x | \gamma) = \gamma_0 e^{-\gamma_1(x - \gamma_2)^2},$$ \hfill (5)

where $\gamma = [\gamma_0, \gamma_1, \gamma_2]$ is a vector of parameters with $\gamma_0, \gamma_1, \gamma_2 > 0$, where $\gamma_0$ controls the maximum number of offspring produced when $x = \gamma_2$ (i.e. age at maximum fecundity), and $\gamma_1$ determines how fast fecundity increases with age. As with mortality, we varied the values of $\gamma$ to simulate a range of fecundity trajectories (Fig. S2). We calculated fecundity for a given age interval as

$$m_x = \int_{x}^{x+\Delta x} m(t) dt.$$ \hfill (6)

With the resulting age-specific fecundity rates and survival probabilities, we constructed Leslie matrices (Leslie, 1945), and calculated the asymptotic population growth rate $\lambda$ as described above, and obtained the corresponding stable age distribution, $v^T = [v_0, v_1, ..., v_\omega]$, where $\omega$ is the age when only 0.1% of the population
remains alive (i.e. \( S(x) = 0.001 \)) (Caswell, 2001).

To investigate discrepancies in the estimation of generation time for measures not considering population growth rates, we adjusted the values of \( m_x \) for all 225 simulated life tables such that the resulting population growth rate could take three values, namely \( \lambda = 0.9, \lambda = 1, \) and \( \lambda = 1.1, \) resulting in 675 populations that were either declining, stationary or increasing.

Calculation of generation time

We calculated generation time \( T_b \) (sensu Leslie, 1966) as the weighted mean age of the mothers at childbirth. We assumed this to be the most appropriate measure of generation time because it requires the least number of assumptions while incorporating all relevant demographic information from the population. We compared \( T_b \) with seven other generation time measures that require data from life tables, population projection matrices or are based on simpler aggregated demographic measures at the species level (Table 1). To compute IUCN’s ‘adult-mortality proxy’, \( T_q \) we calculated the average annual adult mortality (\( \bar{q} \)) as the complement of the average age-specific survival probabilities, \( \bar{p} \), weighted by their stable age-distribution, \( v \) (see above) as

\[
\bar{p} = \sum_{x=0}^{\alpha} \frac{l_x}{l_{x-1}} v_x / \sum_{x=0}^{\alpha} v_x. \tag{7}
\]

For the calculation of IUCN’s ‘reproductive lifespan proxy’, \( T_z \), we used a \( z \) of 0.28 for mammalian and simulated life tables (Keith et al., 2015).

Performance of approximations based on life table information

We fitted linear regression models of the form
\[ \log(T_{ib}) = y_{ib} = \beta_0 + \log(T_y) + \varepsilon, \]  
(8)

with \( \varepsilon_i \sim N(0, \sigma^2) \) for all \( i = 1, 2, \ldots, n \), and all \( j = 1, 2, \ldots, 7 \), where \( n \) is the total number of species, \( \sigma^2 \) is the residual variance, \( T_y \) is generation time for each species \( i \) and approximation \( j \), and \( \hat{y}_{ib} \) are the fitted values. An accurate approximation would result in an intercept \( \hat{\beta}_0 = 0 \), and a slope \( \hat{\beta}_1 = 1 \). We used standard hypothesis testing by means of \( t \)-tests (H0: \( \hat{\beta}_k = \bar{\beta}_k \) for \( k = 0, 1 \)) to determine whether the estimated values of the slope and intercept matched these expectations.

Finally, we calculated root mean square errors (RMSEs) between each approximation and the \( \log(T_{ib}) \) as

\[ \text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} (y_{ib} - \hat{y}_{ib})^2}{n}}. \]  
(9)

**Performance of approximations in the absence of life tables**

We implemented phylogenetic generalized least squares (PGLS) regressions between \( \log(T_{ib}) \) and biological covariates that are more readily available than life tables. We started with the log of body mass in grams \( (m) \), which is allometrically related to \( T_{ib} \) (Gaillard et al., 2005, Cooke et al., 2018), and sequentially added the log of age at first reproduction \( (\alpha) \) and reproductive lifespan \( (r) \) in years, both known to capture demographic variation among mammals (Gaillard et al., 2016). The fully parameterized regression was

\[ \log(T_{ib}) = \overbrace{\beta_0 + \beta_1 \log(m) + \beta_2 \log(\alpha) + \beta_3 \log(r)}^{\delta_0(m, \alpha, r)} + \varepsilon, \]  
(10)

with vector of residuals \( \varepsilon \sim N(0, \sigma^2 \lambda), \Sigma \), where \( \sigma^2 \) is the residual variance of the regression and \( \Sigma \) is the variance-covariance matrix (see Table S2 for coefficients and
Figs S3, S4 for diagnostic plots). Preliminary analyses showed taking the log of $m$, $\alpha$ and $r$ considerably improved the fit of the regression, which is expected from allometric laws (Huxley, 1932) linking life history traits (e.g. all biological times, such as any metric of generation time, scale isometrically on a log-log scale, West, 2017).

The variance-covariance matrix $\Sigma$ is derived from the phylogenetic relationships among the 58 species obtained from the ‘supertree’ phylogeny of Bininda-Emonds et al. (2007). We found the maximum likelihood estimate of the coefficient $\lambda_p$ ($0 \leq \lambda_p \leq 1$) known as Pagel’s lambda, which measures the intensity of the phylogenetic signal (Harvey & Pagel, 1991).

We used the resulting coefficients to estimate the values of $T_{ib}$ as

$$T_i(\cdot) = e^{\hat{\delta}_i(\cdot)} \quad (11)$$

where $T_i(\cdot)$ was the median of $T_{ib}$ under the assumption that $T_{ib}$ is log-normally distributed and $\hat{\delta}_i(\cdot)$ was the fitted value including some or all covariates in equation 10.

We used the Akaike’s information criterion (AIC, Akaike, 1974) for model selection (Table S3), and performed a cross-validation analysis to determine the predictive accuracy of the phylogenetic regression with respect to the z-approximation. We only compared the phylogenetic regression and the z-approximation because, unlike the other generation time proxies, both methods can be used in the absence of life table data. We repeated the analysis for 5000 iterations where, at each iteration, we randomly separated the dataset into a training subset of 53 species, and a validation subset of 5 species. We then fitted the phylogenetic regression in equation 10 to the training set and used the estimated parameters to predict $\log(T_i(m,\alpha,r)) \approx \hat{\delta}_i(m,\alpha,r)$ on the validation set. We then calculated RMSEs on the validation set between the real,
\[ y_{ib}, \text{ and estimated values, } \delta_{i(m,}\alpha,r) \text{, and, for comparison, between the real values and the log of the reproductive lifespan proxy (i.e. } z\text{-approximation), } y_{iz}. \]

**Red List mock assessments**

To illustrate the influence of the different approximations on IUCN Red Listing we conducted mock assessments under Criterion A (IUCN, 2017b). The criterion applies only to declining populations ($\lambda < 1$) for which three generation times exceed 10 years. Given these constraints, we were only able to conduct mock assessments for ten out of the 58 populations. For population reduction, we chose thresholds defined under subcriteria A2-A4, because they represent the most commonly used criteria featuring generation time. For each species $i$, we calculated the proportional decline based on reduction of population size after $t = \text{three generations as}$

\[ N_{it} = \lambda_{i}^t N_{i0}, \tag{12} \]

for all $i = 1,2,\ldots, n$, assuming $N_{i0} = 100$. We emphasize that our results do not represent a full Red List assessment nor do they reflect the true conservation status of that population. It solely serves the purpose of illustrating how choosing different generation time measures could potentially influence the assessment.

We performed all calculations and analyses using the free-open-source software R (R Core Development Team, 2017). For the phylogenetic regressions, we used the R package ‘ape’ v.4.1 (Paradis, Claude & Strimmer, 2004).

**Results**

**Performance of approximations based on life table information**

Generation time measures excluding $\lambda$ differed from $T_b$ (Fig. 1, Table S4). Differences were most severe in the simulated life tables and less pronounced in the observed
mammalian life tables. Generation time was underestimated for decreasing populations ($\lambda < 1$) and overestimated for increasing populations in measures neglecting $\dot{N}$ ($\lambda > 1$, Fig. 1, $T_s$, $T_{sc}$, $T_q$). From observed mammalian life tables, $\dot{N}$ ranged from 0.78 to 1.28 with a mean of 1.02. In simulated life tables, over- or under-estimation in $T_s$ increased in longer-lived species (Fig. 1h).

Furthermore, the assumption of constant demographic rates over the lifetime led to considerable estimation differences (Fig. 1, $T_c$). This was primarily driven by constant $m_c$ (Fig. 1, $T_c$, $T_{cm}$, $T_{sc}$), leading to strong underestimation of generation time in shorter-lived mammals and overestimation of longer-lived species in simulated data. The assumption of constant survival had a considerably lower effect (Fig. 1, $T_{cp}$). In most cases, the regression analysis yielded statistically significant deviations in both estimated intercepts and slopes from the expected values of 0 and 1, respectively (Table 2). Exceptions were the intercepts of $T_s$ and $T_q$ for the real data, and the intercept of $T_c$ for the simulated data. Only $T_z$ on the real data did not display detectable deviations in both parameters, although deviations were both statistically significant for the simulated data.

Comparison of RMSEs across different approximations of generation time for mammals (Table 2) showed that $T_s$ performed best on the real data while $T_{cp}$ performed best on the simulated data.

Performance of approximations in the absence of life tables

The phylogenetic regression between body mass and $T_{bh}$ ($T(m)$) had the highest AIC (AIC = 70.3, $R^2 = 0.45$, $\lambda_p = 0.89$), where $T_b$ was markedly overestimated for shorter-lived species and strongly under-estimated for longer-lived species (Fig. 2). The model with the lowest AIC only included age at first reproduction and reproductive lifespan.
(AIC = -11.3, $R^2 = 0.94$, $\lambda_p = 0.1$, RMSE = 0.178). However, the cross-validation analysis showed that the approximation based on the full phylogenetic regression performed best of all phylogenetic regressions, and at least as well as the $z$-approximation (Fig. 3). For more information on model selection see also Table S3 and Fig. S5.

**Red List mock assessments**

In the assessment of population reduction according to criterion A, errors in generation time led to considerable changes in the IUCN threat status in most species. Generally, extinction risk was underestimated when using generation time approximations, reducing the threat status in many cases (Fig. 4).

**Discussion**

We show that generation time measures are sensitive to the population growth rate $\lambda$ and to the amount of age-dependence in the vital rates. Assuming stationary populations ($\lambda = 1$) or constant fecundity with age resulted in over- or under-estimation in generation time even when high-quality life table data were available. For instance, measures assuming stationary populations over-estimated generation time for populations with $\lambda > 1$, and under-estimated generation time when $\lambda < 1$. These biases simply resulted from the scaling of $T_b$ by the reciprocal of $\lambda$ (i.e. $1/\lambda$; Table 1). Some of the generation time proxies often used for threat assessments could be inaccurate, except for the reproductive lifespan proxy, $T_z$, which provides a close approximation when accurate data on age at first reproduction and reproductive lifespan are available. However, when expanding the set of age-specific vital rates with simulated data, this proxy’s accuracy diminishes drastically (Fig. 1m).
The generation time metrics described in the IUCN guidelines are cohort-based and therefore do not account for non-stationarity of populations. This assumption is rarely met as illustrated by our analysis of 58 wild mammalian populations and leads to over- or under-estimation even when populations are only slightly increasing or decreasing. While $T_b$ assumes that the population is at the stable age distribution, which might not apply to many populations, using $T_s$ on cross-sectional data assumes not only stable age structure, but also stationarity.

The IUCN guidelines explicitly mention that estimating generation time in populations displaying strong age-dependence in vital rates is especially difficult (IUCN, 2017b). Concurrently, we found substantial errors when assuming constant vital rates with age involving a downward bias from mammalian life tables, particularly when assuming constant fecundity with age. Also, Dillingham (2010) showed that the incorrect assumption of constant fecundity with age led to an underestimation of generation time and thereby to overharvesting of birds.

Considering extinction risk assessments, underestimation of generation time is especially worrisome because it can lead to wrongly assigning a species to a lower risk category (Fig. 4). Our simulations showed larger errors for longer-lived species, which are particularly vulnerable to extinction due to their slow life histories and long generation times (e.g. Cardillo et al., 2005).

Of the two IUCN proxies, $T_z$ outperformed $T_q$ and performed especially well in mammals for which we estimated ages at first reproduction directly from the life tables. However, for most species, this information is unavailable and estimates are likely to be more severely biased. This is evident from the analysis on simulated data, where $T_z$ performed poorly. As previously suggested (Fung & Waples, 2017), $T_z$ might only be useful when $z$ estimates for species with similar life history are available.
Contrary to our findings in mammals, Fung and Waples (2017) found that $T_z$ generated higher errors than $T_g$, when compared to the cohort proxy, $T_c$ which, as we explain here, is not the most appropriate metric of generation time. Additionally, they calculated average mortality $\bar{p}$ based on the geometric mean between the survival at $\alpha$ and $\omega$ (i.e. $(l_\omega / l_\alpha)^{1/(\omega - \alpha)}$). We advise against using the geometric mean since it strongly depends on the mortality rates observed at first and last reproduction and is only valid for species with constant survival with age. Constant survival has not been recorded in mammals (see e.g. Gaillard et al., 2017) and has only been reported in few species of aquatic invertebrates and plants (Roach & Gampe, 2004; Daňko, Kozłowski & Schaible, 2015).

The estimation of generation time from phylogenetic regression on body mass alone did not provide reliable results across mammals but may provide some useful information if only body mass is available for the focal species. Cooke et al. (2018) showed that body mass and phylogeny are reliable predictors of generation time across Bovidae species; thus body mass might improve the estimation of generation time among closely related species. We found that including two biological times, age at first reproduction and reproductive lifespan, improved the prediction (Fig. 2). The full model requires a similar amount of information (it does not require $z$, but includes body mass) as the reproductive lifespan proxy, $T_z$, but is more consistent with general life-history theory as it predicts generation time from species-specific values. Furthermore, it can facilitate using available information from related species in the estimation of generation time.

We assumed life tables provide accurate species-specific generation time measures, but this metric can vary considerably within a species. Empirical studies have revealed an almost twofold variation in generation time within a given
mammalian species (e.g. from 3.93 to 6.80 years in roe deer (*Capreolus capreolus*, Nilsen et al., 2009), or from 2.3 to 3.6 years in wild boar (*Sus scrofa*, Servanty et al., 2011)). This further stresses that the cohort approach to calculate generation time needs to be evaluated carefully, particularly for populations exhibiting large variation in vital rates due to cohort environmental effects (e.g. Gaillard et al., 1997; Le Galliard, Marquis & Massot, 2010; Gaillard et al., 2016). To benefit extinction risk assessments, studies investigating intra- vs. inter-specific variation, and variation in relation to environmental changes and increasing stressors, such as harvesting and climate change will be required.

Even the best estimation methods are only as good as the data used. A challenge will be to fill the glaring data gaps of demographic knowledge occurring even among some of the best-studied taxa. Efforts to collect age and stage-specific data across the tree of life, e.g. the COMADRE Animal Matrix Database (Salguero-Gómez et al., 2016), will continue making these data available, as illustrated in the increasing publication record of vital rates since the 1960s (Fig. S6). Moreover, the exploration of new data sources such as captive data from the Zoological Information Management System (ZIMS), with standardized information for over 10 million individuals from 21,000 species (Species360, 2018), can provide knowledge for threatened species where field data is not yet available.

Until we are able to gather sufficient demographic information for a wide range of species to estimate key demographic traits such as generation time, we will have to rely on proxies such as those provided in the IUCN guidelines. Based on our findings, we provide the following recommendations:

1. We recommend $T_b$ as the complete measure of generation time to be included in the IUCN guidelines.
2. We further recommend alerting assessors of our results, such as the underestimation of generation time resulting from the assumption of constant $m_x$ and clear guidelines on the calculation of average vital rates.

3. To spur initiatives for further research on generation time it would be desirable to include data and methods used for the estimation of generation time, where this is appropriate, in the online database of Red List assessments (http://www.iucnredlist.org).

Further knowledge on generation times is urgently needed to design effective conservation management and prioritize species at greatest risk.

Authors’ contributions

FC, JS, DAC, and JMG conceived and designed the study; JMG, VR, and JFL collected the data; JS and FC analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

All data were sourced from the published literature and citations to all sources are provided. R code for the simulation of survival and fecundity trajectories and
calculation of generation time proxies is available at:


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### Tables:

#### Table 1: Methods to estimate generation time

<table>
<thead>
<tr>
<th>Generation time formula</th>
<th>Description</th>
<th>Assumptions</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_s = \frac{\sum x \lambda^{-1} m_x}{\sum \lambda^{-1} m_x}$</td>
<td>Mean age of the parents of offspring produced in the current time period once the population has reached the stable age distribution *‡</td>
<td>Population at its stable (stage distribution, overlapping generations.</td>
<td>(Leslie 1966; Caswell 2001)</td>
</tr>
<tr>
<td>$T_i = \frac{\sum x l_x m_x}{\sum x l_x}$</td>
<td>Mean age at which members of a cohort of newborns produce offspring*</td>
<td>Applied to cohort life tables or stationary populations ($\lambda=1$).</td>
<td>(Dublin &amp; Lotka 1925; Caswell 2001)</td>
</tr>
<tr>
<td>$T_A = \log \frac{R_0}{\log \lambda}$</td>
<td>Time required for the population to grow by the net reproductive rate, $R_0$</td>
<td>Population at its stable (stage distribution</td>
<td>(Birch, 1948; Caswell, 2001)</td>
</tr>
<tr>
<td>$T_d = \frac{\lambda x v w}{v F w}$</td>
<td>Average time between two reproductive events in the family tree of a population*¶</td>
<td>Population at its stable (stage distribution, matrix entries are normalized (sum to 1)</td>
<td>Bienvenu &amp; Legendre, 2015</td>
</tr>
<tr>
<td>$T_c = \frac{\sum x \lambda^{-1} p^+}{\sum \lambda^{-1} p^+}$</td>
<td>As in $T_s$ but with constant fecundity and survival model*</td>
<td>Constant survival and fecundity from onset of breeding</td>
<td>(Niel &amp; Lefebvre, 2005; Gaillard et al., 2005)</td>
</tr>
<tr>
<td>$T_{op} = \frac{\sum x \lambda^{-1} p^+ m_x}{\sum \lambda^{-1} p^+ m_x}$</td>
<td>As in $T_s$ but with constant survival, varying fecundity model*</td>
<td>Constant survival from onset of breeding, fecundity can vary</td>
<td>(Dillingham, 2010)</td>
</tr>
<tr>
<td>$T_{op}' = \frac{\sum x \lambda^{-1} p' m_x}{\sum \lambda^{-1} p' m_x}$</td>
<td>As in $T_s$ but with constant survival, varying survival model*</td>
<td>Constant fecundity, survival can vary</td>
<td></td>
</tr>
<tr>
<td>$T_{op}'' = \frac{\sum x \lambda^{-1} l_x}{\sum \lambda^{-1} l_x}$</td>
<td>As in $T_s$ but with constant fecundity and survival model* for stationary populations</td>
<td>Constant survival and fecundity, stationary populations.</td>
<td></td>
</tr>
<tr>
<td>$T_{op}' = \frac{\sum x p^+}{\sum x}$</td>
<td>As in $T_s$ but with constant fecundity and survival model*</td>
<td>Constant survival and fecundity from onset of breeding; $q$ and $\alpha$ are well known</td>
<td>(IUCN, 2017b)</td>
</tr>
<tr>
<td>$T_q = \frac{\sum x l_x}{\sum x}$</td>
<td>As in $T_s$ but with constant fecundity and survival model*</td>
<td>Reproductive-lifespan proxy*</td>
<td>(IUCN, 2017b)</td>
</tr>
<tr>
<td>$T_q = \frac{\sum x l_x}{\sum x}$</td>
<td>Adult-mortality proxy*</td>
<td>$\alpha$, $\omega$ and $\alpha$ are well known</td>
<td></td>
</tr>
</tbody>
</table>

* $x =$ age, $l_x =$ probability of surviving to age $x$, $m_x =$ number of female offspring born to females at age $x$, $\lambda =$ population growth rate at its stable (st)age distribution, $p =$ mean annual survival, $q =$ mean annual mortality, $\alpha =$ age at first reproduction, $\omega =$

*‡ when population distribution is age-specific

*¶ when population distribution is constant
age at last reproduction, \( z \) = species-specific constant. For \( \omega = \infty \), \( T_c \) becomes \( T_c = \alpha + 642\frac{p}{(\lambda - p)} \) (Gaillard et al., 2005) and \( T_q \) becomes \( T_q = \alpha + 1/q \) (IUCN, 2017b).

† The denominator in \( T_b \) is necessary to account for small errors in the estimation of the continuous Euler-Lotka equation from a discrete approximation.

‡ \( R_0 = \sum l_i m_i \)

¶ \( F \) = fecundity matrix of population projection matrix, \( v \) reproductive value (left-eigenvector) of population projection matrix, \( w \) stable (st)age distribution (right-eigenvector) of population projection matrix
Table 2: Results of the regression analysis and root mean square errors (RMSE) between $T_b$ and the different approximations for 58 mammalian life tables (upper panel) and simulated life tables (lower panel). Values include estimated regression coefficients with standard errors in parentheses, $p$-values for the hypothesis described in the methods, and ranks based on RMSEs.

<table>
<thead>
<tr>
<th>Approx.</th>
<th>Intercept ($SE$)</th>
<th>Slope ($SE$)</th>
<th>$p$-val. Interc.</th>
<th>$p$-val. Slope</th>
<th>RMSE</th>
<th>$R^2$</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Real data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_s$</td>
<td>0.05 (0.04)</td>
<td>0.95 (0.02)</td>
<td>0.225</td>
<td><strong>0.028</strong></td>
<td>0.132</td>
<td>0.97</td>
<td>1</td>
</tr>
<tr>
<td>$T_c$</td>
<td>1.10 (0.05)</td>
<td>0.71 (0.04)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.879</td>
<td>0.88</td>
<td>7</td>
</tr>
<tr>
<td>$T_{cp}$</td>
<td>0.23 (0.04)</td>
<td>0.92 (0.02)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.163</td>
<td>0.97</td>
<td>2</td>
</tr>
<tr>
<td>$T_{cm}$</td>
<td>0.91 (0.04)</td>
<td>0.77 (0.03)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.682</td>
<td>0.94</td>
<td>5</td>
</tr>
<tr>
<td>$T_{sc}$</td>
<td>1.13 (0.07)</td>
<td>0.61 (0.04)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.861</td>
<td>0.79</td>
<td>6</td>
</tr>
<tr>
<td>$T_z$</td>
<td>0.06 (0.06)</td>
<td>1.01 (0.03)</td>
<td>0.297</td>
<td>0.98</td>
<td>0.186</td>
<td>0.95</td>
<td>3</td>
</tr>
<tr>
<td>$T_q$</td>
<td>0.28 (0.17)</td>
<td>0.73 (0.08)</td>
<td>0.112</td>
<td><strong>0.001</strong></td>
<td>0.578</td>
<td>0.62</td>
<td>4</td>
</tr>
<tr>
<td><strong>Simulated data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_s$</td>
<td>0.26 (0.03)</td>
<td>0.89 (0.01)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.272</td>
<td>0.85</td>
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</tr>
<tr>
<td>$T_c$</td>
<td>0.05 (0.05)</td>
<td>1.15 (0.03)</td>
<td>0.337</td>
<td>$&lt; 0.001$</td>
<td>0.493</td>
<td>0.72</td>
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</tr>
<tr>
<td>$T_{cp}$</td>
<td>0.02 (0.01)</td>
<td>0.98 (0.01)</td>
<td><strong>0.020</strong></td>
<td>$&lt; 0.001$</td>
<td>0.068</td>
<td>0.99</td>
<td>1</td>
</tr>
<tr>
<td>$T_{cm}$</td>
<td>0.12 (0.06)</td>
<td>1.13 (0.03)</td>
<td><strong>0.028</strong></td>
<td>$&lt; 0.001$</td>
<td>0.524</td>
<td>0.69</td>
<td>5</td>
</tr>
<tr>
<td>$T_{sc}$</td>
<td>0.55 (0.06)</td>
<td>0.88 (0.03)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.545</td>
<td>0.58</td>
<td>6</td>
</tr>
<tr>
<td>$T_z$</td>
<td>0.60 (0.10)</td>
<td>0.58 (0.04)</td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.001$</td>
<td>0.857</td>
<td>0.28</td>
<td>7</td>
</tr>
<tr>
<td>$T_q$</td>
<td>0.30 (0.07)</td>
<td>0.93 (0.03)</td>
<td>$&lt; 0.001$</td>
<td><strong>0.023</strong></td>
<td>0.481</td>
<td>0.54</td>
<td>3</td>
</tr>
</tbody>
</table>
**Figure 1:** Comparison between $T_b$ and seven generation time approximations. Generation time calculated from 58 life tables of mammalian populations (a-g), and from life tables constructed from simulated data (h-n) on log-log-scale. The grey dashed line represents isometry (i.e. the equation $y = x$). The black solid line shows the fitted regression of the data points. The grey shaded areas correspond to standard errors. Colour and shape indicate population growth rates. For interpretability we inverted the axes whereby log($T_b$) is on the x-axis and log($T_j$) on the y-axis.

**Figure 2:** Relationship between $T_b$ and generation time fitted values from three phylogenetic generalized least squares. PGLS include either body mass only ($T(m)$), age at first reproduction and reproductive lifespan ($T(\alpha, r)$), or body mass, age at first reproduction, and reproductive lifespan ($T(m, \alpha, r)$). Linear regression (on log-log scale) was fitted to life tables from 58 mammalian populations. The black dashed line represents isometry (i.e. the equation $y = x$). The red solid line represents the best regression line fitted to the data points. Grey shaded areas correspond to standard errors.

**Figure 3:** Boxplots of the RMSE between the log($T_{ib}$) and the predicted $\delta(m, \alpha, r)$ values ($T(m, \alpha, r)$, left) and the z-approximation log($T_{iz}$) ($T_z$, right) on the validation set.
Figure 4: Influence of generation time metrics on mock Red List assessments under criterion A. Population reduction is measured over three generations calculated for the different generation time approximations (represented by shapes and colours) for ten mammalian species. Coloured backgrounds show thresholds for Red List categories CR: Critically endangered, EN: Endangered, VU: Vulnerable.
\[ T_b = \frac{\sum_{x=0}^{\omega} x\lambda^{-x} l_x m_x}{\sum_{x=0}^{\omega} \lambda^{-x} l_x m_x} \]

\[ T_q = \frac{\sum_{x=0}^{\omega} \lambda^{-x} l_x}{\sum_{x=0}^{\omega} \lambda^{-x} m_x} \]
\[
T(\alpha, r)
\]

\[
T(m, \alpha, r)
\]

\[
T(m)
\]

\[
T_b
\]

\[
R^2 = 0.94
\]

\[
R^2 = 0.95
\]

\[
R^2 = 0.45
\]
<table>
<thead>
<tr>
<th>Species</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cervus elaphus</td>
<td>EN</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>EN</td>
</tr>
<tr>
<td>Marmota flaviventris</td>
<td>EN</td>
</tr>
<tr>
<td>Kobus leche</td>
<td>EN</td>
</tr>
<tr>
<td>Panthera leo</td>
<td>EN</td>
</tr>
<tr>
<td>Propithecus diadema</td>
<td>EN</td>
</tr>
<tr>
<td>Vulpes vulpes</td>
<td>EN</td>
</tr>
<tr>
<td>Elephas maximus</td>
<td>EN</td>
</tr>
<tr>
<td>Ursus arctos</td>
<td>VU</td>
</tr>
<tr>
<td>Mirounga angustirostris</td>
<td>VU</td>
</tr>
</tbody>
</table>

% Population reduction over three generations:

- **CR**: Critically endangered
- **EN**: Endangered
- **VU**: Vulnerable