Received Date: 09-Feb-2015
Revised Date: 02-Apr-2015
Accepted Date: 19-May-2015
Article Type: Article
MS#14-1990

Article

Improved estimation of intrinsic growth $r_{\max}$ for long-lived species: integrating matrix models and allometry

Improved estimation of intrinsic growth

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Manuscript received 9 February 2015; revised 2 April 2015; accepted 19 May 2015; final version received 9 June 2015.

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Abstract.

Intrinsic population growth rate ($r_{\max}$) is an important parameter for many ecological applications, such as population risk assessment and harvest management. However, $r_{\max}$ can be a difficult parameter to estimate, particularly for long-lived species, for which appropriate life table data or abundance time series are typically not obtainable. We describe a method for improving estimates of $r_{\max}$ for long-lived species by integrating life-history theory (allometric models) and population-specific demographic data (life table models). Broad allometric relationships, such as those between life history traits and body size, have long been recognized by ecologists. These relationships are useful for deriving theoretical expectations for $r_{\max}$, but $r_{\max}$ for real populations may vary from simple allometric estimators for "archetypical" species of a given taxa or body mass. Meanwhile, life table approaches can provide population-specific estimates of $r_{\max}$ from empirical data, but these may have poor precision from imprecise and missing vital rate parameter estimates. Our method borrows strength from both approaches to provide estimates that are consistent with both life-history theory and population-specific empirical data, and are likely to be more robust than estimates provided by either method alone. Our method uses an allometric constant: the product of $r_{\max}$ and the associated generation time for a stable-age population growing at this rate. We conducted a meta-analysis to estimate the mean and variance of this allometric constant across well-studied populations from three vertebrate taxa (birds, mammals, and elasmobranchs) and found that the mean was approximately 1.0 for each taxon. We used these as informative Bayesian priors that determine how much to "shrink" imprecise vital rate estimates for a data-limited population toward the allometric expectation. The approach ultimately provides estimates of $r_{\max}$ (and other vital rates) that reflect a balance of information from the individual studied population, theoretical expectation, and meta-analysis of other populations. We applied the method specifically to an archetypical petrel (representing the genus *Procellaria***)** and to white sharks (*Carcharodon carcharias*) in the context of estimating sustainable fishery bycatch limits.

Key words:
allometric (rT) models; Bayesian analysis; demography; integrated population models; intrinsic growth rate; life-table models; long-lived species; population dynamics; Procellaria; white shark, Carcharodon carcharias.

Introduction

The intrinsic rate of increase is the maximum potential exponential growth rate that a population can achieve under optimal resource conditions in its environment (Caughley 1977). It is a key parameter for understanding life-history evolution and population dynamics, and is important in many conservation applications. Intrinsic growth and related terms have been variously defined in the literature (e.g., r_{max}, r_{m}, $r_{\text{intrinsic}}$, $\bar{r}$; Caughley 1977, Niel and Lebreton 2005, Gedamke et al. 2007, Fagan et al. 2010). For practical application purposes, our interest is the maximum growth rate that would be possible for a real-world, low-density population (e.g., a small founding group, or one in early stages of recovery from severe depletion) with a stable age distribution in a broadly favorable natural environment, which we refer to as r_{max}. In wildlife and fisheries management, r_{max} may be used for projecting population recovery times, conducting population viability analyses, or estimating exploitation or removal rates that correspond to management targets or thresholds. For example, many species of marine megafauna are impacted by incidental catch (or bycatch) from fisheries (Lewison et al. 2004, Moore et al. 2013). For these data-poor species, the intrinsic growth rate is a fundamental parameter for estimating incidental fishery-catch limits (Moore et al. 2013) and conducting certain types of Ecological Risk Assessments (ERAs) based on the use of Productivity and Susceptibility Analyses (PSAs) (Cortés et al. 2010, Hobday et al. 2011).

Unfortunately, intrinsic growth rates are difficult to estimate for many species or populations, particularly for many long-lived, data-limited species in need of active management. For example, under the U.S. Marine Mammal Protection Act, bycatch mortality to a marine mammal population must be below an estimate of Potential Biological Removal (PBR) or else management procedures to reduce bycatch must be initiated. PBR is calculated as a function of population abundance and intrinsic growth rate estimates (Wade 1998, Taylor et al. 2000). The latter is unknown for most populations, so default values are typically used (0.04 for cetaceans, 0.12 for pinnipeds), but the appropriateness of these defaults has not been fully evaluated. Obtaining species- or population-specific estimates of the intrinsic growth rate would therefore improve the PBR management scheme.

Intrinsic growth rates may be estimated directly or through model-based approaches. Direct estimation requires fairly long time series (relative to generation time) of abundance estimates for fast-growing (e.g., recovering) populations whose growth rates are not yet limited by resource availability and that have age distributions at least close to the stable age distribution. Where these circumstances exist, regression methods for estimating average growth rate as a function of time or population abundance are straightforward to implement (e.g., Eberhardt and Simmons 1992, de Valpine and Hastings 2002, Morris and Doak 2002, Sibly et al. 2005, Clark et al. 2010). However, such data are not usually available, particularly for certain types of species, e.g., the long-lived and late-maturing marine species that motivate our research, whose age as first reproduction can be >10 years and life spans are decades. Such species are particularly sensitive to human impacts on survival rates (Heppell et al. 1999, 2005). For these species, direct estimates of intrinsic growth generally require decades of data, usually from well-monitored populations recovering from intensive human exploitation after effective conservation measures have been put in place (e.g., Best 1993, Balazs and Chaloupka 2004). Few large marine vertebrate populations fit these criteria. Therefore, despite any limitations from simplifying assumptions (e.g., simplified biology, ignoring density dependence or senescence), model-based approaches to estimating $r_{\max}$ are more common and more practical, at least for these types of species.

In the wildlife demography literature, there are two general classes of model-based methods for estimating $r_{\max}$ or $\lambda_{\max} = \exp(r_{\max})$ for most populations of long-lived species: analysis of life table methods, and life-history theory and allometric scaling relationships. For purposes of the current analysis, we refer to life table methods in the sense of calculating $r_{\max}$ from estimates of annual survival and reproductive rates (in presumably nonlimiting resource conditions) using matrix algebra methods (e.g., eigenanalysis or solving the characteristic equation; Caswell 2001) or solving the discrete form of the Euler-Lotka equation (for good methodological overviews, see Skalski et al. 2008, Fagan et al. 2010). Allometric methods use empirically verified relationships across species within broad taxonomic groups between demographic rates (e.g., survival rates, life span, age at maturity) and organismal characteristics (namely body size or metabolic rate) to make inference about population growth rate from relatively few input parameters (e.g., Hennemann 1983, Savage et al. 2004*a*, *b*, Niel and Lebreton 2005, Hone et al. 2010). Both approaches have been used to assess risk for long-lived populations. For example, PSAs for sharks have used estimates of $\lambda_{\max}$ derived from matrix models (Cortés 2002, Simpfendorfer et al. 2008, Cortés et al. 2010), whereas allometric models have been used in developing estimates of potential biological removal (PBR) for birds (Niel and Lebreton 2005, Dillingham and Fletcher 2008, 2011, Dillingham 2010, Richard and Abraham 2013).

The two types of model-based approaches have individual advantages, but also individual shortcomings. The advantage of using life table methods is that estimates of $r_{\max}$ account for age-structured demographic rates and these are empirically informed for the population of interest. However, it is difficult to know whether field measures of demographic rates correspond to those that would be observed for a population growing at $r_{\max}$ (Gedamke et al. 2007, Fagan et al. 2010). Parameterizing a matrix model (or Euler-Lotka equation) may also be hampered by data limitations (error in parameter estimates) and structural uncertainties about the life history schedule (i.e., matrix dimensionality and how many parameters to include); see Heppell et al. (2000) and Lynch and Fagan (2009).

The advantage of using allometric methods is that these require fewer variables than life table or matrix model approaches and fewer data from the particular study population. Rather, $r_{\max}$ estimates are informed by well-established evolutionary relationships between, for example, body size and various demographic rates. However, these methods are equally sensitive to input parameter uncertainty and only provide theoretical or expected value estimates of population growth (e.g., given an estimate of body size or age at maturity). As a result, an allometric approach can fail to fully account for population- or species-level variation in demographic complexity, given that individual populations are expected to deviate from the "archetype" (Savage et al. 2006, Ginzburg et al. 2010). For example, Hone et al. (2010) found for mammals a strong relationship between field estimates of population growth rates and age at maturity, but growth rates for individual species could not be predicted precisely from the relationship. Moreover, there remains uncertainty in allometric scaling relationships (Duncan et al. 2007) due, at least in part, to methodological difficulties or inconsistencies in empirically testing the underlying theories (Fagan et al. 2010).

We present a general approach that draws on the strengths of both types of model-based methods to provide estimates of $r_{\max}$ that are consistent with both allometric theory and population-specific empirical data, and that may therefore be more robust than estimates provided by either method alone.

Methods

Background

For long-lived species in particular, estimates of $r_{\max}$ from either life table or allometric methods are strongly influenced by estimates of maximum adult survival. However, the bias in $r_{\max}$ (from error in survival estimates) occurs in opposite directions for the two types of methods, a fact that we exploit in our model development. For matrix models, higher survival values lead to higher $r_{\max}$ values when other demographic parameters remain constant. Across species, however, many parameters are correlated, and allometric models show that species with higher survival rates generally have lower $r_{\max}$ values because of the evolutionary trade-off between survival (s) and reproductive output (Williams 1966, Charnov 2005). For populations that are impacted by anthropogenic mortality (e.g., bycatch in fisheries, hunting), use of empirical estimates of s will either underestimate $r_{\max}$ (e.g., matrix models) or overestimate $r_{\max}$ (e.g., allometric models) (Dillingham and Fletcher 2008). The differences between the two methods can be striking, highlighting the potential risk from using empirical estimates of adult survival to estimate $r_{\max}$ using either method alone. For the petrel example described in Table 1, treating an empirical estimate of survival that incorporates substantial bycatch mortality (s = 0.89; Barbraud et al. 2008) as if it represented maximum survival would yield estimates of $r_{\max}$ = 0.088 using a particular allometric model (demographic invariant method, DIM; Niel and Lebreton 2005) and $r_{\max}$ = 0.006 using a matrix model. For some species (e.g., sharks), little is known about adult survival, and either method would perform poorly. More generally, when there is parameter uncertainty, each method can produce estimates of $r_{\max}$ discordant with the other: e.g., allometric estimates of $r_{\max}$ that require breeding success rates > 1 or similar impossibilities, or matrix model estimates of $r_{\max}$ that are strongly inconsistent with ecological allometric theory. The approach we describe in this paper is to analytically identify combinations of demographic parameters that produce matrix model estimates that are also consistent with observed allometric relationships.

The particular allometric relationship we use is the approximate constancy (invariance) of the product of r_{max} and the associated generation length (in years) for a stable-age population growing at r_{max}. This generation length has previously been termed the "optimal" generation length because generation time depends on conditions, but r_{max} occurs when conditions are optimal (Niel and Lebreton 2005); e.g., high survival combined with relatively early age at first reproduction as might occur in resource-replete conditions for a low-density population. Indicative of the general nature of this relationship, we denote optimal generation length using a generic symbol (T_{opt}) not tied to any specific calculation; however, our actual calculations were based on optimal mean generation length ($\bar{T}_{\mathrm{op}} = \sum_{i=1}^{\infty} i l_i f_i$, where l_i is the survival probability from birth to age i and f_i is the annual fecundity at age i; Leslie 1966, Niel and Lebreton 2005), as it is relatively insensitive to senescence (Niel and Lebreton 2005), which is difficult to model for the data-poor populations included in this study. The approximate constancy of $r_{\mathrm{max}}T_{\mathrm{opt}}$ is based on multiplying distinct allometric relationships for each variable. Allometric relationships are of the form $p = aM^{x}$, where M is body mass, p is some characteristic, and a and x are constants; these describe broad trends observed across species. Quarter-power exponents are common in allometry (Savage et al. 2004*b*), and for r_{max} and T_{opt} the exponents are near −0.25 and 0.25, respectively. Multiplying the two allometric relationships leads to the expected relationship previously described (Lebreton 1981, Fowler 1988, Charnov 1993, Niel and Lebreton 2005):

$$r_{\mathrm{max}}T_{\mathrm{opt}} \approx a_{rT} \quad (1)$$

where $a_{rT} = a_r a_T$ and a_r, a_T are the constants in the allometric equations for intrinsic growth rate and generation time, respectively. The constancy of a_{rT} is assumed to hold within homogenous taxonomic groups independent of body mass, but may vary between taxa. For example, Niel and Lebreton (2005) demonstrated that $r_{\mathrm{max}}T_{\mathrm{opt}} \approx 1$ for 13 well-studied bird species (from diverse taxa and spanning a large range in body sizes) whose populations were assumed to be growing under nonlimiting resource conditions.

Niel and Lebreton (2005) and Dillingham (2010) combined Eq. 1 with specific population models that allow estimation of $r_{\max}$ with limited demographic data for archetypical populations. For example, Niel and Lebreton (2005) use a simple age-based matrix model where adult survival (s) and fecundity (f, female offspring per female per year) are constant from the age at first reproduction (α), referred to as the constant-fecundity model (Dillingham 2010). For a matrix of this form, mean generation time (Leslie 1966) reduces to $T = \alpha + s/(\lambda - s)$ (Niel and Lebreton 2005) and, combined with the allometric model, provides the equation for the demographic invariant method, DIM (Lebreton 2005, Dillingham 2010):

$$\lambda_{\max}^{\mathrm{DIM}} = \exp\left[a_{rT} \left(\alpha + s_{\mathrm{opt}} / \left(\lambda_{\max}^{\mathrm{DIM}} - s_{\mathrm{opt}} \right) \right)^{-1} \right]. \quad (2)$$

In this context, α should represent the age at first reproduction under nonlimiting resource conditions. If a_{rT} is known (e.g., for birds, $a_{rT} \approx 1$; Niel and Lebreton 2005), then intrinsic growth can be calculated, at least approximately, with minimal demographic data using Eq. 2. That is, due to the structure of the matrix model and the requirement that $r_{\max} T_{\mathrm{opt}} = 1$ (for birds), the only demographic parameters required to calculate $r_{\max}$ or $\lambda_{\max}$ are α and s; all other parameters are implied by the model. Dillingham (2010) derived similar equations for a more biologically realistic model (termed the varying-fecundity model) that allows fecundity to increase over a number of age classes, but requires some additional information on fecundity. Dillingham (2010) also noted that the varying-fecundity model can be approximated by the constant-fecundity model if α represents a typical (e.g., near the mean or median) age at first reproduction rather than the earliest age that some animals reproduce.

Our analysis has two parts. First, we develop two new methods to estimate $r_{\max}$ by integrating matrix and allometric (i.e., $r_{\max} T_{\mathrm{opt}}$ invariance) models. Second, we use empirical data to examine the constancy of $r_{\max} T_{\mathrm{opt}}$ for mammals and sharks in an effort to evaluate the taxonomic generality of the relationship that was demonstrated for birds by Niel and Lebreton (2005); the outputs of this meta-analysis are needed to apply the estimation methods to real populations.

The first $r_{\max}$ estimation method, which we term the rT-exact method for an rT-ideal population, describes the population growth of an archetypical population. This method assumes that the population follows the allometric model exactly. We show how straightforward computational methods allow us to generalize the approaches of Niel and Lebreton (2005) and Dillingham (2010) to allow other matrix population models to be used, estimate the expected value for $r_{\max}$ even when a point estimate of optimal (i.e., maximum) adult survival (s_{opt}) is unavailable, and incorporate all available demographic information to inform results. The second method, termed the *rT*-adjusted method, incorporates estimates of process variance (population-level variation) in the $r_{\max}T_{\mathrm{opt}}$ relationship, appropriate for describing individual rather than archetypical populations. For this method, we use allometric relationships to improve the precision of matrix model results by adjusting estimates toward *rT*-exact estimates and generating more realistic estimates of uncertainty in $r_{\max}$, but still allow individual populations to vary from the allometric expectation. To demonstrate the applicability and utility of these two new methods, we include a demonstration application of our approach to two case studies regarding management and population viability of an archetypical pelagic seabird (petrels of the genus *Procellaria*) and white sharks (*Carcharodon carcharias*).

Model development

The two new $r_{\max}$ estimation methods rely on simple variants of Eq. 1. The first method, the *rT*-exact method, describes $r_{\max}$ for an archetypical, or *rT*-ideal, population, where Eq. 1 is exact. Thus for *rT*-ideal populations:

$$r_{\max}T_{\mathrm{opt}} = a_{rT}. \quad (3)$$

Although the *rT*-exact method is useful to describe growth rates for archetypical populations, slight departures from this relationship are expected for individual populations. To allow individual populations to vary from Eq. 1, we can assume that the variability is normally distributed and model the product of intrinsic growth and optimal generation time as

$$r_{\max}T_{\mathrm{opt}} \sim N\left(a_{rT}, \sigma_{rT}\right) \quad (4)$$

where a_{rT} is the allometric constant and σ_{rT} is the population-level standard deviation, which describes the amount of true variation across populations around the theoretical prediction for $r_{\max}T_{\mathrm{opt}}$. Although Eq. 4 has advantages of simplicity, it does theoretically allow $r_{\max}T_{\mathrm{opt}} < 0$. For combinations of a_{rT} and σ_{rT} where negative values are a concern (e.g., a_{rT} is less than approximately $2\sigma_{rT}$ from 0), a log-normal or truncated normal distribution could be used in place of Eq. 4.

The *rT*-exact method.—

The *rT*-exact method combines matrix models with Eq. 3 in order to predict $r_{\max}$ for an archetypical population. Given demographic parameters representative of maximal population growth, matrix model (MM) estimates $r_{\max}^{\mathrm{MM}}$ and $T_{\mathrm{opt}}^{\mathrm{MM}}$ are calculated, e.g., using the Euler-Lotka equation and the equation for mean generation time (Dillingham 2010), along with their product $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$. If $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$ equals a_{rT}, then the population is *rT*-ideal; otherwise, it is not. Simply, the *rT*-exact method requires that the matrix model is fully concordant with the allometric model.

Niel and Lebreton (2005) and Dillingham (2010) both presented special cases of the *rT*-exact method. For illustration, assume a population that follows the constant-fecundity model where s_{opt} is the only unknown parameter. For both DIM and matrix models, $r_{\max}$ is then simply a function of s_{opt}. The relationship between model estimates of s_{opt} and $r_{\max}$ for DIM (i.e., Eq. 2) and the matrix model for this illustrative population is shown in Fig. 1a. As s_{opt} increases, $r_{\max}$ increases for the matrix model (dashed line), but decreases for DIM (solid line). Because s_{opt} is unknown, neither method can calculate $r_{\max}$ exactly. However, the point in Fig. 1a where these lines intersect is where the matrix and DIM models agree, and is the solution for s_{opt} and $r_{\max}$ from the *rT*-exact method. In short, this new approach finds the values of s_{opt} and $r_{\max}$ (using numerical methods) where $r_{\max}T_{\mathrm{opt}}$ from the matrix model equals the allometric constant a_{rT}.

A more generic computational approach for *rT*-ideal populations is to (1) put prior distributions on all parameters, (2) simulate a large number of matrix models, and (3) then calculate the product of growth and generation time ($r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$) for each; and finally, (4) keep those iterations that satisfy the allometric theory constraint of $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}} = a_{rT}$ (within an allowed numerical tolerance, i.e., $\left|r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}} - a_{rT}\right| \le \delta$ for some small δ) and form the posterior distribution for $r_{\max}T_{\mathrm{opt}}$. For data-rich populations, there may be relatively little uncertainty in $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$, whereas for data-poor populations, the uncertainty would be large. Thus, uncertainty about $r_{\max}$ will reflect uncertainty in demographic rates but parameters will be constrained by asserting that the population must be *rT*-ideal. For the illustrative population shown in Fig. 1, if there was uncertainty in parameters in addition to s_{opt}, matrix model methods would produce a range of possible growth rates for each value of *s*. Eq. 3 would be satisfied for all parameter sets that produce combinations of α, s_{opt}, and $\lambda_{\max}$ that also satisfy Eq. 2. Fig. 1b shows realizations of 1000 simulated matrix models that are *rT*-exact (within $\delta = 0.05$).

The *rT*-adjusted method.—

The *rT*-adjusted method estimates population growth for individual populations by combining matrix models with Eq. 4. This method relaxes the *rT*-ideal constraint and only assumes that $r_{\max}T_{\mathrm{opt}}$ is near a_{rT}, allowing for population-level variation from the ideal. The first three steps of the computational approach are the same as for the *rT*-exact method (i.e., simulating and calculating values for the matrix models). For the *rT*-adjusted method, step (4) is to simulate $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}}$ from the allometric model (A) (e.g., Eq. 4). Eq. 4 is appropriate for the allometric model as long as $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}} > 0$ for the vast majority of iterations; otherwise, a log-normal or truncated-normal model could be used instead. In step (5), those iterations where $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$ is near $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}}$ (i.e., $\left|r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}} - r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}}\right| \le \delta$) are kept and others discarded. For the constant-fecundity population described in Fig. 1, matrix model estimates that fall near Eq. 2 are kept with increasing probability (Fig. 1c), but no longer must lie on Eq. 2. In Supplement 1, implementation of the *rT*-exact and *rT*-adjusted methods is described for the illustrative population in Fig. 1.

The tolerance, δ, sets the allowable numerical error, where smaller values equate to higher precision but increased computational time. Based on $a_{rT} \approx 1$ for birds (Niel and Lebreton 2005), $\delta \le 0.05$ provides a reasonable balance between speed and precision (e.g., for a population with generation time $T_{\mathrm{opt}} = 10$ years, this corresponds to error of ± 0.005 in $r_{\max}$ for any individual iteration, with overall error reduced by the total number of iterations), whereas $\delta \le 0.01$ is appropriate for high-precision applications or populations with lower generation times. The resulting, integrated estimates (I) of intrinsic growth, generation time, and their product ($r_{\max}^{\mathrm{I}}$, $T_{\mathrm{opt}}^{\mathrm{I}}$, and $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{I}}$) are derived from posterior intervals of the simulation, whereas the integrated distribution for maximum annual growth ($\lambda_{\max}^{\mathrm{I}}$) is calculated by transforming quantiles of $r_{\max}^{\mathrm{I}}$. As a diagnostic, we also examine the distributions of $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$ and $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}}$, where limited overlap could be used as a model diagnostic, potentially indicating flawed model assumptions, data errors, or an unusual population.

Estimating allometric parameters for birds, mammals, and sharks

We gathered data for birds, mammals, and sharks to estimate allometric parameters for each group. Niel and Lebreton (2005) noted that Eq. 1 could be rewritten as $\log r_{\max} = \log T_{\text{opt}} \quad \log a_{rT}$. They therefore modeled the data as $\mathrm{E}\left(\log r_{\max}\right) = \beta \log T_{\text{opt}} + \log a_{rT}$ and ran a regression to test the assumption of $\beta = -1$. The authors then estimated a_{rT} by back-transforming the intercept in a revised model with the slope forced to −1. Eq. 4 is a similar but simpler model and is a natural extension of Eq. 1. Further, it eliminates potentially difficult choices about which regression method to use (e.g., ordinary least squares (OLS), major axis, or standardized major axis; for discussion, see Warton et al. 2006, O’Connor et al. 2007). However, the log–log regression provides an easy way to examine relationships not evident from Eq. 4. For example, in an allometric analysis of basal metabolic rate and mass, Kolokotrones et al. (2010) were able to find previously undetected curvature and a body temperature effect by using regression methods within a log–log regression.

We therefore modeled data using both the log–log regression and the simpler method based on Eq. 4. The log–log regression was designed to examine general linearity and whether the slope was near −1, and Eq. 4 was used to actually estimate a_{rT} and σ_{rT}. Because the first method was used for basic diagnostics only, rather than adjusting the degrees of freedom or otherwise modeling phylogenetic dependence, we simply note that the standard error of the slope from OLS estimates may be underestimated if the dependence is strong, but other values (e.g., the estimated slope and R^2) are appropriate for estimating $r_{\max}$ conditional on T_{opt} (O’Connor et al. 2007). We also note that the corresponding estimate of σ_{rT} from Eq. 4 will include the intrinsic population-level variability (i.e., process error) that we are interested in, but also includes measurement error and possible sources of model-based bias. Therefore, the actual population-level variability is probably $< \hat{\sigma}_{rT}$.

For birds, we used the data from Niel and Lebreton (2005). For mammals, we used empirical $r_{\max}$ estimates from count data for fast-growing populations for 41 out of 64 species compiled by Duncan et al. (2007), including 10 orders of mammals and ranging in size from rodents and lagomorphs to elephants and baleen whales. Data for the other 23 species did not satisfy inclusion measures for our analysis (briefly, $r_{\max} < 2$, $\alpha > 0.5$, and $s < 1$ when calculated by the characteristic equation; see Appendix A for details). We compiled female age at first reproduction and fecundity estimates from other published databases for the mammals (Ernest 2003, Jones et al. 2009, Tacutu et al. 2013), with the merged data available in Supplement 2 for the 41 included species. To calculate generation time, survival estimates are also required. However, age- or stage-specific survival estimates were not available, so we assumed a single annual survival rate through life and found this rate by solving the characteristic equation for *s*: $\lambda^{\alpha} - s\lambda^{\alpha-1} - fl_{\alpha} = 0$, where $\lambda = \exp(r)$ and $l_{\alpha} = s^{\alpha}$. The simplifying assumption of a single survival rate is a suitable proxy for age-structured survivorship for purposes of estimating *r* and allometric relationships (Lynch and Fagan 2009). We then estimated optimal generation time as $T_{\text{opt}} = \alpha + s/(\lambda - s)$ (assuming α, *s*, were estimated for optimal or near-optimal conditions) using the mean generation length (Leslie 1966) and an assumption of constant fecundity from age at first reproduction (Niel and Lebreton 2005, Dillingham 2010), and performed a log–log analysis, sensu Niel and Lebreton (2005) to estimate the regression slope and confirm that it was close to −1. We then used the simpler Eq. 4 to estimate the allometric parameters.

For sharks, we used estimates of growth and generation time from matrix models presented by Cortés (2002). Developing matrix models for sharks is challenging due to the lack of empirical survival estimates for this taxon. In their place, Cortés (2002) used indirect estimators developed primarily using data for teleosts, whose application to elasmobranchs has not been empirically justified (Kenchington 2013). Cortés (2002) combined several different estimators and used the differences between them as one approach to estimating uncertainty in survival. Therefore, the estimates for sharks have greater measurement error and potential sources of bias than the estimates for birds or mammals. Although the values from Cortés (2002) may be broadly interpreted as estimates of intrinsic growth, we recognize their limitations. For example, some estimates of intrinsic growth were <0, and estimates of uncertainty were conditional on the assumed models for survival. We thus analyzed the data to look for general consistency with the log–log analysis and Eq. 4 and general similarities in parameter estimates between sharks, birds, and mammals. Using only those populations where the estimate of $r_{\max} > 0$ led to 32 of 41 populations in Cortés (2002) for inclusion in the log–log analysis. Because Cortés (2002) provided uncertainty estimates for population growth rates, we were able to perform an additional analysis to estimate mean a_{rT} and the population-level variation in this parameter (σ_{rT}) by adjusting for measurement error in $r_{\max}$ (see Appendix A for details).

Case studies

The *rT*-exact method for petrels.—

Many petrel species (Family Procelliidae) are listed as threatened by the International Union for Conservation of Nature (IUCN) due to incidental capture (bycatch) in fishing gear (BirdLife International 2013). Because of these impacts, empirical estimates of survival, where available, incorporate anthropogenic mortality and therefore do not represent potential maximum survival. For example, recent survival estimates for the White-chinned Petrel (*Procellaria aequinoctialis*) are very low (<0.90) compared to similar, less impacted species (Barbraud et al. 2008). One solution is to use survival estimates from congeneric species at lower risk from bycatch (e.g., Barbraud et al. 2009, Dillingham and Fletcher 2011) to estimate $r_{\max}$ or $\lambda_{\max}$, and recognize that the estimates may be biased as a result or treated as an approximation. As an alternative approach, we demonstrate the *rT*-exact method for an archetypical *Procellaria* species.

In this example, we compare estimates of $\lambda_{\max}$ from matrix, DIM (i.e., Eq. 2), and *rT*-exact methods ($\lambda_{\max}^{\mathrm{MM}}, \lambda_{\max}^{\mathrm{DIM}}$, and $\lambda_{\max}^{rTe}$), and also estimate optimal survival using the *rT*-exact method (s_{opt}^{rTe}). Our purpose is to compare the sensitivities of $\lambda_{\max}$ to a_{rT} and the demographic parameters among the three models to identify those parameters that, for a given level of error, most influence point estimates of $\lambda_{\max}$. By combining knowledge of sensitivities with estimates of parameter uncertainty, this type of analysis can help a researcher to determine which model is most appropriate for their data; for example, models that are sensitive to parameters that have large associated uncertainties would be expected to perform poorly.

We first built a matrix population model for a generic *Procellaria* species. We then selected parameter values by examining relevant species-specific estimates available from primary or secondary sources (Brooke 2004, Barbraud et al. 2008, Fletcher et al. 2008, Dillingham et al. 2012, ACAP 2013, BirdLife International 2013), with specific details described in Appendix A. The resulting matrix was then used to estimate s_{opt} and $\lambda_{\max}$ using the *rT*-exact method, assuming $a_{rT} = 1$ based on the estimate from Niel and Lebreton (2005). The *rT*-exact estimate of s_{opt} was used for the matrix model and DIM approaches to estimate $\lambda_{\max}$. Sensitivities of $\lambda_{\max}$ to model parameters were then calculated using numerical derivatives.

The *rT*-adjusted method for white sharks.—

To demonstrate the *rT*-adjusted method, we built a matrix population model for the eastern north Pacific population of white shark. In 2012, this population was petitioned for listing under the U.S. Endangered Species Act. The National Oceanic and Atmospheric Administration (NOAA) convened a Biological Review Team (BRT) of government scientists to evaluate relevant scientific information and provide an assessment report (Dewar et al. 2014) that the Agency used to determine whether the white shark should be listed as a threatened or endangered species (the decision was to not list the species; 78 Federal Register 40104–40127). The population viability analysis for the BRT assessment was partially based on estimates of $r_{\max}$, derived using our methods as presented here. We began by building a demographic matrix model for the white shark, but parameter uncertainty meant that matrix model results, by themselves, were unsatisfactorily imprecise. Therefore, in combination with the matrix model, we used the estimates of allometric parameters (a_{rT}, σ_{rT}) for sharks (i.e., based on our analysis of the data from Cortés (2002)), informed by estimates from the other taxa, which had higher data quality, to provide *rT*-adjusted estimates of intrinsic growth.

Few vital rates are known precisely for white sharks, but variously informative priors can be placed on all key parameters (see Appendix A for details). Drawing parameters from these distributions provides a prior distribution for matrix model parameters $r_{\max}T_{\mathrm{opt}}{}^{\mathrm{MM}}$ that does not take the allometric model into account. To incorporate the allometric model, we matched each matrix model draw with one from the allometric model ($r_{\max}T_{\mathrm{opt}}{}^{\mathrm{A}}$), but used a log-normal distribution in place of Eq. 4 so that $r_{\max}T_{\mathrm{opt}} > 0$. Similarly, we accounted for uncertainty in σ_{rT} by sampling from a log-normal distribution with a CV based on our analysis of the Cortés shark data (Cortés 2002). Those iterations where the allometric and matrix models agreed formed the integrated, *rT*-adjusted posterior distribution.

Analyses were performed using R 3.0.1 (R Development Core Team 2013). For the Bayesian analysis of the Cortés (2002) shark data, the OpenBUGS variant (version 3.2.2; Thomas et al. 2006) of BUGS (Lunn et al. 2000) was linked to R using the R2WinBUGS library (Sturtz et al. 2005), with estimates based on four chains of 260000 iterations with the first 10000 iterations discarded and thinning set to 100, with good convergence diagnostics and low Monte Carlo error.

Results

Estimating allometric parameters for birds, mammals, and sharks.—

All three taxonomic groups showed strong relationships between $r_{\max}$ and T_{opt} (Fig. 2), with R^2 from the log–log regression equal to 0.96, 0.91, and 0.72 for birds, mammals, and sharks, respectively. In each case, the estimated slope was close to −1, with estimated slopes (and 95% confidence interval) equal to −0.93 ± 0.12 (birds), −0.99 ± 0.10 (mammals), and −0.96 ± 0.46 (sharks). Both R^2 and precision were lowest for sharks, which was expected, given the uncertainties in the matrix model estimates of $r_{\max}$ for them.

The allometric constants were similar for all three taxa, with $a_{rT} \approx 1$. Estimates of a_{rT} from Eq. 4 were 1.07 ± 0.09 (birds), 1.17 ± 0.09 (mammals), and 0.97 ± 0.25 (sharks). The associated standard deviations, σ_{rT}, were estimated as 0.15 (birds), 0.30 (mammals), and 0.69 (sharks), accounting for all sources of noise (i.e., population-level variability and measurement error, as well as any model-based bias). When using the Bayesian model to adjust for measurement error for sharks, $\hat{a}_{rT} = 0.84$ (95% credible interval 0.65 to 1.05) and the remaining error reduces to $\hat{\sigma}_{rT} = 0.41$ (0.23 to 0.61). For an animal with a generation time of 10 years or more, this suggests that variation in $r_{\max}$ among populations is probably <0.04 for any of these taxa.

Case study 1: petrels.—

For the rT-ideal population based on the demography of *Procellaria* petrels, we treated s_{opt} as unknown and other parameters as known, and calculated rT-exact estimates of population growth ($\lambda_{\max}^{rT\text{e}}$) and optimal survival ($s_{\text{opt}}^{rT\text{e}}$). Using $s_{\text{opt}}^{rT\text{e}}$ in a matrix model and DIM (Eq. 2) allowed us to compare sensitivities of three point estimators ($\lambda_{\max}^{rT\text{e}}, \lambda_{\max}^{\text{MM}}, \lambda_{\max}^{\text{DIM}}$) to demographic parameters to analyze approximate model performance. The rT-exact estimate of the maximum growth rate when $a_{rT} = 1$ is $\lambda_{\max}^{rT\text{e}} = 1.070$ (or $r_{\max}^{rT\text{e}} = 0.068$) and the corresponding estimate of optimal survival is $s_{\text{opt}}^{rT\text{e}} = 0.947$. The estimates of λ_{max} and s_{opt} are very similar to those presented by Dillingham and Fletcher (2011), who estimated $s_{\text{opt}} \approx 0.94$ using empirical data from a number of petrel species and $\lambda_{\text{max}} \approx 1.074$ using DIM.

For the *rT*-exact method where s_{opt} is unknown, intrinsic growth was most sensitive to a_{rT} and the proportion breeding (k), and least sensitive to age at maturity, α (Table 1). Sensitivities were always smaller when using the *rT*-exact method compared to the matrix model or DIM for shared parameters. Hence, relative model performance depends on sensitivities and uncertainties for those parameters not in common. Compared to the matrix model, the impact on λ_{max} of error in s_{opt} of 0.01 in the matrix model is equivalent to the impact of error in a_{rT} of 0.15 in the *rT*-exact method, if the other parameters were known without error. Compared to DIM estimates, the *rT*-exact method has three additional parameters (c_1, c_2, which are the ratios of younger age-class survival rates to adult survival, and k; see Appendix A) not used by DIM, while DIM has one parameter (s_{opt}) not used by the *rT*-exact method. Because the *rT*-exact method is insensitive to c_1, c_2, and k, and DIM is highly sensitive to s_{opt}, error of 0.10 in each of c_1, c_2, and k (in the worst case where all errors are in the same direction) has the equivalent impact of error of 0.016 in s_{opt}. From a management perspective, this means that the *rT*-exact method would be expected to outperform DIM in most settings. The exceptions would be where c_1, c_2, and k are highly uncertain or where s_{opt} is measured with high precision.

Case study 2: white sharks.—

Distributions for λ_{max} from the matrix model only, allometric model only, and the *rT*-adjusted method that integrates both models are in Fig. 3. For this example, we set $a_{rT} = 1$ and sampled from a log-normal distribution with average population-level variation $\sigma_{rT} = 0.4$ (see Appendix A for details). The value $a_{rT} = 1$ is consistent with the estimate from either Eq. 4 or the Bayesian model that adjusted for measurement error for sharks (see Appendix A), as well as the value for the other taxa with higher quality data. The *rT*-adjusted distribution reflects uncertainty in matrix model parameters, but constrains the uncertainty so that Eq. 4 is satisfied. While still allowing for population-level variability, Fig. 3 shows the constrained distribution that results from incorporating allometric trends with the matrix model. The *rT*-adjusted posterior distribution for λ_{max} for white sharks has a mean of 1.050, SD = 0.017, and 95% credible interval of 1.022 to 1.091. By comparison, the distribution of $\lambda_{\max}$ for the matrix model alone had a mean of 1.059, SD = 0.028, included negative values, and had a substantially wider 95% credible interval (1.008 to 1.114) that included unrealistically small values. The variance for the *rT*-adjusted distribution was only 37% that of the variance for the matrix model (i.e., $0.017^2/0.028^2 = 0.37$), contains no negative values, and the credible interval represents a more plausible range, showing the benefits of the *rT*-adjusted model compared to a matrix model for this case study.

Discussion

Generating robust estimates for demographic parameters and $r_{\max}$, in particular, for long-lived species is a priority for both ecological research and conservation applications. Estimating intrinsic growth from matrix models provides population-specific estimates, but precision can be unsatisfactory when important demographic parameters such as survival are unavailable or measured with low precision. Here, we have presented two new methods that combine demographic information used for matrix models with broader ecological understanding garnered from empirical allometric relationships to generate improved estimates of intrinsic growth rates. The first (*rT*-exact) method provides estimates of intrinsic growth for what we call an *rT*-ideal population (e.g., the expected growth rate for an archetypical population with a particular combination of adult survival and maturation age). The second (*rT*-adjusted) method acknowledges that species may vary from some theoretical expectation and thus incorporates process error in the allometric constant (a_{rT}) to generate distributions for intrinsic growth that reflect this natural variability. These methods can be applied generally, but are especially applicable for data-poor populations, for which neither matrix models nor allometric models are fully satisfactory. As our case studies demonstrate, our methods provide biologically meaningful inferences about species life history parameters, and can inform conservation and management.

As with all models, our approach depends on empirically validating the theoretical prediction with data; i.e., that the product $r_{\max}T_{\mathrm{opt}}$ is approximately invariant. Our meta-analysis of data for birds, mammals, and sharks indicates that the theory is well-supported across several taxa with expected $r_{\max}T_{\mathrm{opt}} \approx 1$ across the full range of generation lengths included in the data sets. Data types and the amount of data used to evaluate this taxonomic generality varied by taxon. For birds, $r_{\max}$ estimates were generated from matrix models for rapidly growing populations for which high-quality demographic data were available, and a broad suite of taxa were represented (Niel and Lebreton 2005). Estimates for $r_{\max}$ for mammals were based on count data for dozens of rapidly increasing populations, although the data set was taxonomically biased toward certain orders with relatively high growth rates (e.g., many ungulate and carnivore species, few bats or primates). For sharks, $r_{\max}$ was calculated from matrix models that relied on multiple indirect survival estimators derived for teleosts (Cortés 2002). These differences suggest that estimates of the allometric constants are most reliable for birds and least reliable for the data-poor sharks. For the *rT*-adjusted method, quantifying population-level variation σ_{rT} and accounting for that variation in predictive models is also required. For birds and mammals, relatively high-quality data suggest that estimates of σ_{rT} primarily reflect the population-level variation that we are interested in, but still incorporate some amount of measurement error. For sharks, we were able to separate some of the measurement error from population-level variation by adding an additional component to our model, but overall data quality was lowest for this taxon.

Given available data and the limited number of taxa studied, it is unknown whether $a_{rT} \approx 1$ is general across all animal taxa or whether the similarities between values for these taxa were coincidental or only apply to relatively long-lived species (noting that taxa characterized by truly rapid growth potential such as teleosts or insects were not included in the analysis, nor were mammals that mature younger than 1 year and have multiple litters per year). It is also unclear whether the larger estimate of σ_{rT} for sharks was a result of model-based bias and uncertainty, or possibly represents additional variation caused by greater phylogenetic diversity or poikilothermy in that taxon. This suggests two areas of future research: (1) examining additional taxonomic groups to better explore the generality of our findings, and (2) determining the effect of model-based assumptions (e.g., from the use of indirect survival estimates) on the estimates of the allometric parameters for sharks.

The *rT*-exact method, designed to estimate intrinsic growth for a typical population by combining all available demographic data with knowledge of allometric patterns, was found to yield robust estimates of $r_{\max}$ for a long-lived seabird, even when important demographic parameters (e.g., survival) are poorly known. In fact, although our focus is on estimating $r_{\max}$, we note that this method also can be used to estimate optimal survival and other demographic parameters. Compared to methods such as DIM or matrix models that rely heavily on estimates of adult survival for long-lived populations, the *rT*-exact method is relatively insensitive to its parameter inputs and therefore error in any one has limited impact on the estimate of $r_{\max}$. We primarily focus on the effect of survival due to its importance in DIM and matrix models, but estimation of other demographic parameters can be challenging for long-lived species (e.g., age at first reproduction). In settings where survival is estimated well and other parameters poorly, the *rT*-exact method would yield essentially the same estimates as DIM when using the constant-fecundity model. For data-poor populations that have reproductive information available, and where estimates of survival are poor or impacted by unquantified anthropogenic mortality, the *rT*-exact method would perform especially well compared to the others. DIM and matrix methods risk large bias in $r_{\max}$ when s_{opt} is measured poorly, whereas the *rT*-exact method reduces this risk by taking advantage of the opposite directions of those biases. This is especially important in conservation settings that use reference point (e.g., mortality limit) estimators based on $r_{\max}$. For example, PBR, which has also been adapted for seabirds and sea turtles (Dillingham and Fletcher 2008, 2011, Curtis and Moore 2013, Richard and Abraham 2013), includes the parameter $R_{\max} = \exp(r_{\max}) - 1$, and is <0.10 for many of the long-lived marine megafauna to which it is applied (Moore et al. 2013). Small errors in $R_{\max}$ translate to large proportional errors in the PBR, and therefore can have large management impacts (Dillingham 2010).

The second method that we present, the *rT*-adjusted method, extends the first by focusing on individual rather than archetypical populations. Although the *rT*-exact method is useful for predicting how we expect an archetype to behave and may be sufficient for many applications, these predictions may not be sufficiently accurate for individual populations that differ from the expectation, in which case population-level variation in $r_{\max}$ with respect to $r_{\max}T_{\text{opt}}$ must be accounted for. For these settings, the *rT*-adjusted method uses allometric patterns to adjust matrix model estimates of population growth toward the allometric ideal, but still allows for variation from it. The amount of adjustment depends on the distance between matrix model estimates of $r_{\max}T_{\text{opt}}$ and the allometric constant, the precision of matrix model estimates, and the normal level of variation from the ideal expected within a taxon. Although our analyses provide initial estimates for σ_{rT} for three taxa, these estimates include sampling variance and thus overestimate population-level variance. Future research that improves the precision of these estimates would make these methods even more useful.

Like any method, these methods should be used with care. Although the primary purpose of the rT-adjusted method is to improve precision of $r_{\max}$ estimates by using all available data, it also naturally removes inconsistencies between allometric and matrix models. However, inconsistencies could highlight data or model errors, or an interesting population that does not follow the allometric trend. For example, inconsistencies between allometric and matrix models could be a relatively simple way to identify whether the survival estimate used is potentially suboptimal. We therefore recommend that estimates from matrix and allometric models be compared to each other and to the integrated estimates from the rT-adjusted method (as shown in Fig. 3 for white sharks) as part of a quality control process.

Acknowledgments

Funding for this project was provided from the Lenfest Ocean Program. Ideas for this paper were originally presented at a workshop hosted by the Southwest Fisheries Science Center, 5–7 December 2012, entitled “Calculating productivity and related estimates for sharks,” and we thank the participants for their helpful input. J. Barlow and T. Eguchi provided detailed comments that improved the manuscript. We thank S. Heppell and anonymous reviewers for their comments and suggestions.

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Supplemental Material

Ecological Archives

The Appendix and Supplements 1 and 2 are available online: http://dx.doi.org/10.1890/14-1990.1.sm

Fig. 1. The inverted relationship between optimal adult survival (s_{opt}) and intrinsic growth ($r_{\max}$) for matrix and allometric models can be used to predict $r_{\max}$. The allometric model states that the product of intrinsic growth and optimal generation time ($r_{\max}T_{\mathrm{opt}}$) is approximately a constant (a_{rT}). When $r_{\max}T_{\mathrm{opt}} = a_{rT}$ (Eq. 3) (a, b), we term this an rT-ideal population and consider it to represent an archetypical population. In (a), s_{opt} is the only unknown, whereas in (b, c) there is uncertainty in multiple parameters. In (a), the rT-exact solution (single dot) occurs where the matrix model solution (dashed line) intersects the allometric solution (solid line, the demographic invariant method, DIM; Niel and Lebreton 2005). In (b), multiple demographic parameter combinations from the matrix model within a small tolerance ($\delta = 0.05$) of DIM are rT-exact (black dots) while others (gray dots) are not. In (c), the rT-adjusted method allows individual species to deviate from being rT-ideal ($r_{\max}T_{\mathrm{opt}} \sim N(\mu, \sigma^2$; Eq. 4), with iterations near

DIM more likely to be accepted (black dots) than not (gray dots), but populations are not required to be *rT*-ideal.

Fig. 2. Log–log regressions of optimal generation time (T_{opt}) vs. maximum growth rate (r_{max}) for (a) birds, (b) mammals, and (c) sharks. The regression slopes were set to −1, as predicted by Eq. 1, and the regression fit only the intercepts.

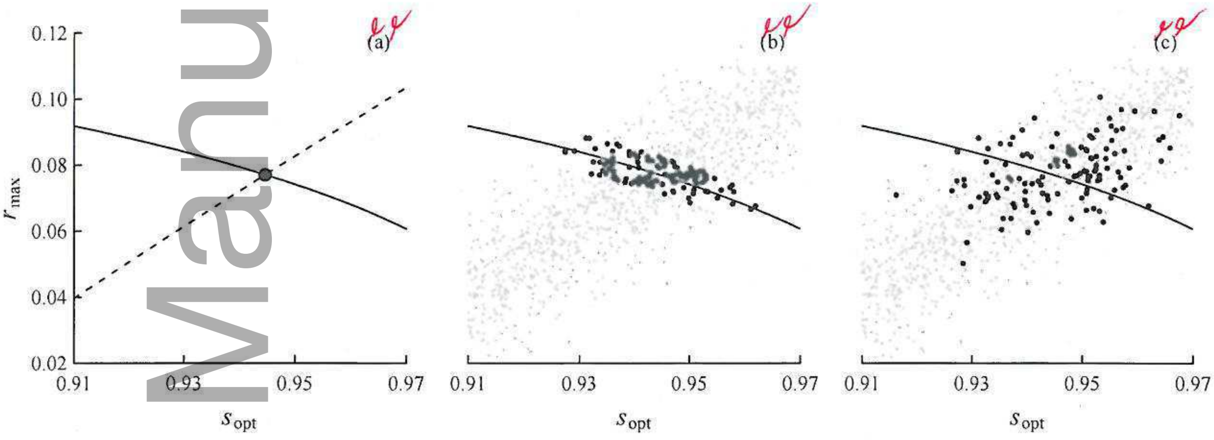
Fig. 3. Distributions for λ_{max} for white sharks using matrix model (black), DIM (open), and *rT*-adjusted (gray) methods. Distribution of matrix model estimates solely reflects measurement uncertainty in matrix model parameters. Expected λ_{max} values from the allometric-based DIM are calculated using the estimator of Niel and Lebreton (2005) and incorporate population variability from the allometric constant ($a_{rT} = 1$, $\sigma_{rT} = 0.4$, $CV(\sigma_{rT}) = 0.35$, generated from a log-normal distribution) as well as uncertainty in age at first reproduction (α) and optimal adult survival (s_{opt}). The distribution from the *rT*-adjusted method accounts for uncertainty in all demographic parameters, adjusting for allometric patterns and population variability.

Table 1. Sensitivity of λ_{max} to the allometric constant (a_{rT}), adult survival (s), ratios of breeding success and juvenile survival to adult survival (c_1, c_2), age at first reproduction (α), and proportion of adults breeding (k) for an archetypical *Procellaria* sp. petrel using three types of models.

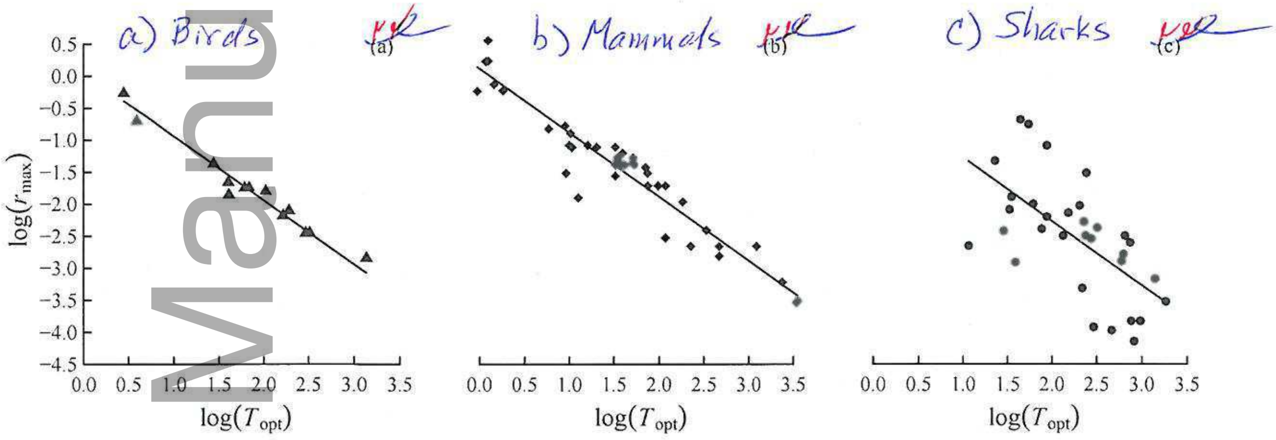
Parameter	Model type		
	Matrix	DIM	*rT*-exact
a_{rT}	na	0.106	0.073
s	1.130	−0.512	na
c_1	0.091	na	0.028
c_2	0.081	na	0.025
α	−0.009	−0.008	−0.008
k	0.097	na	0.030

Notes: DIM denotes the demographic invariant method. Sensitivities were calculated based on the values $a_{rT} = 1$, $s = 0.947$, $c_1 = 0.8$, $c_2 = 0.9$, $\alpha = 7$, and $k = 0.75$.

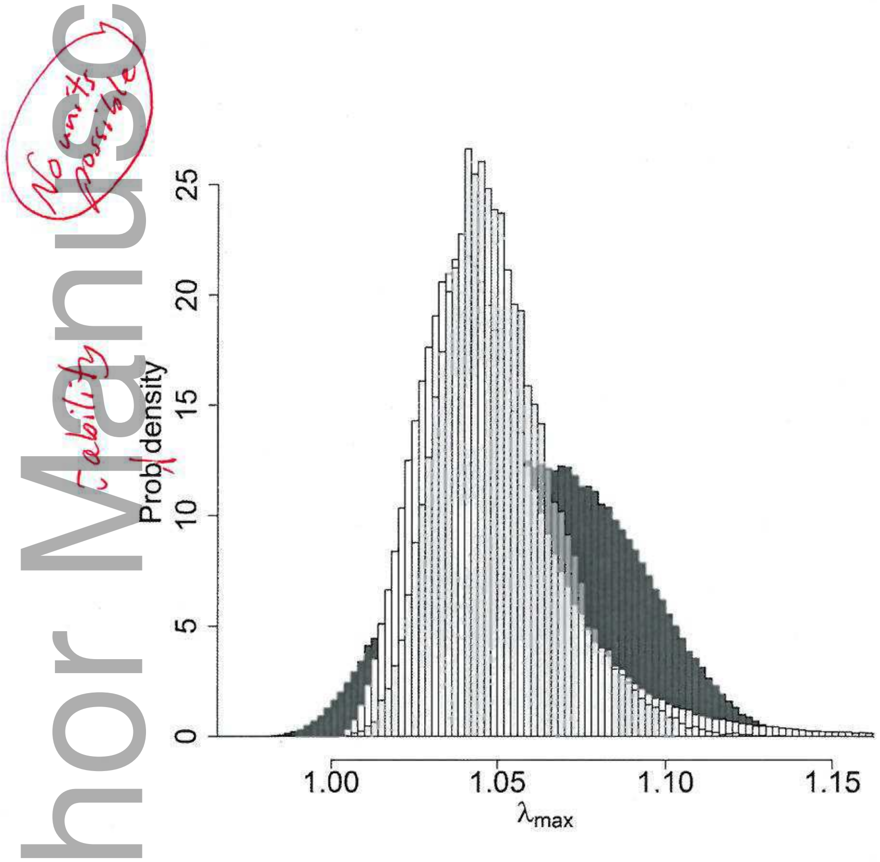
Dillingham
14-1990
Fig 1

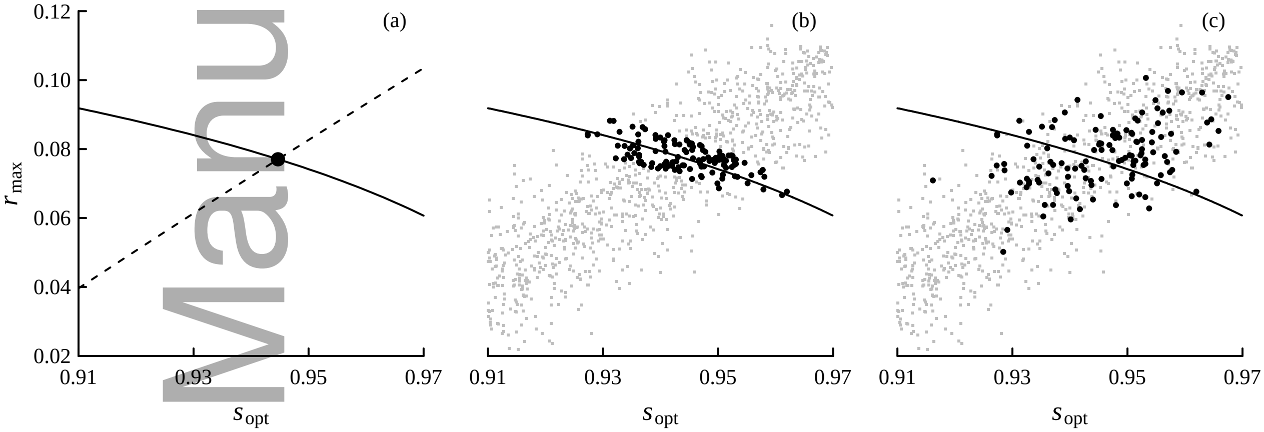


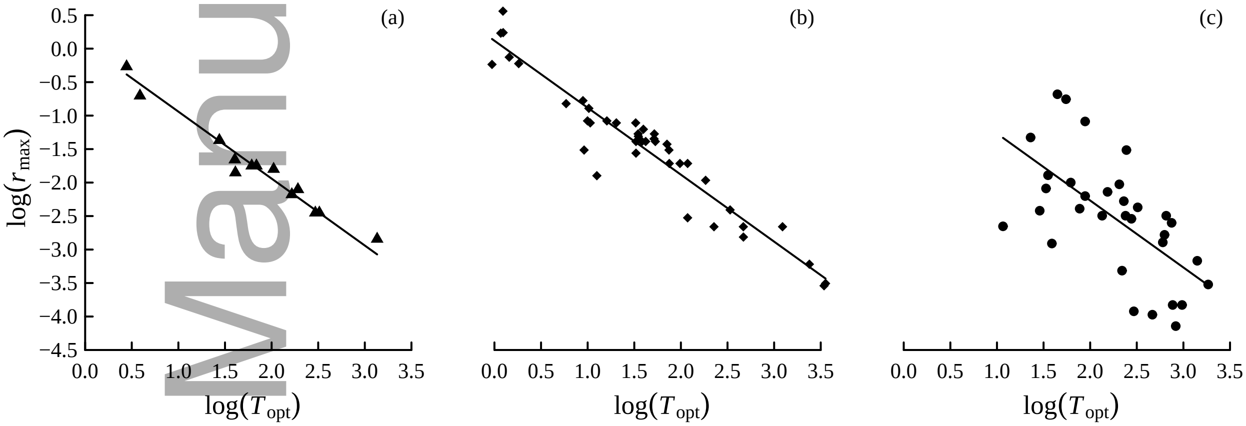
Dillingham
14-1990
Fig 2

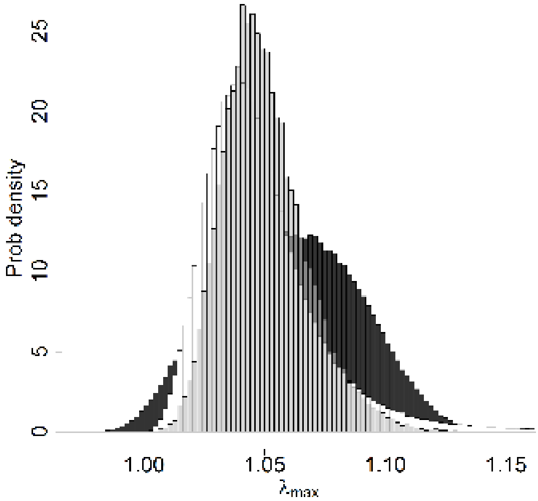


Dillingham
14-1990
Fig 3




(a)
(b)
(c)
$r_{\max}$
0.12
0.10
0.08
0.06
0.04
0.02
0.91
0.93
0.95
0.97
s_{opt}


(a)
(b)
(c)
0.5
0.0
−0.5
−1.0
−1.5
−2.0
−2.5
−3.0
−3.5
−4.0
−4.5
log($r_{\max}$)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
log(T_{opt})



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